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Neural Dynamics during Binocular Rivalry: Indications from Human Lateral Geniculate Nucleus

1 **Title:** Neural dynamics during binocular rivalry: Indications from human lateral geniculate

2 nucleus

3 **Abbreviated Title:** Rivalry in LGN

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18

24   **Abstract**

25   When two sufficiently different stimuli are presented to each eye, perception alternates between

26   them. This binocular rivalry is conceived as a competition for representation in the single stream

27   of visual consciousness. The magnocellular (M) and parvocellular (P) pathways, originating in

28   the retina, encode disparate information, but their potentially different contributions to binocular

29   rivalry have not been determined. Here, we used functional magnetic resonance imaging (fMRI)

30   to measure the human lateral geniculate nucleus (LGN), where the M and P neurons are

31   segregated into layers receiving input from a single eye. We had three participants (1 male, 2

32   females) and used achromatic stimuli to avoid contributions from color opponent neurons that

33   may have confounded previous studies. We observed activity in the eye-specific regions of LGN

34   correlated with perception, with similar magnitudes during rivalry or physical stimuli

35   alternations, and also similar in the M and P regions. These results suggest that LGN activity

36   reflects our perceptions during binocular rivalry and is not simply an artifact of color opponency.

37   Further, perception appears to be a global phenomenon in the LGN, not just limited to a single

38   information channel.

39   **Significance Statement**

40   Multiple channels of visual information emerge from the retina, but their role in our visual

41   perception remains unclear. Binocular rivalry is an interesting phenomenon in that the separate

42   stimuli presented to each eye remain stable, yet our conscious perception alternates between

43   them. We tested whether both the magnocellular and parvocellular visual streams contribute to

44   binocular rivalry. We measured their activations during binocular rivalry in the human lateral

45   geniculate nucleus, where these two streams are physically disjoint. We found that unperceived

46   information in both streams was suppressed during binocular rivalry, suggesting that both the

47   magnocellular and parvocellular streams have a role in our conscious perception.

48   **Neural dynamics during binocular rivalry: Indications from human lateral geniculate**

49   **nucleus**

50   Binocular rivalry (BR) occurs when each eye is presented with a sufficiently different stimulus,

51   resulting in a competition of these monocular stimuli for perception (Alais and Blake, 2015;

52   Blake, 2022), and, typically, alternating perception between the two stimuli. BR provides a

53   means to study visual awareness in the brain (Rees, 2009; Blake et al., 2014), because perception

54   can be decorrelated from the physical stimulus. Here, we investigated the neural mechanisms of

55   BR, focusing on the lateral geniculate nucleus (LGN), the visual relay in the thalamus, and its

56   eye-specific and M and P layers (see Figure 1).

57   In BR, it has been unclear whether the stimuli are competing for perception (Leopold and

58   Logothetis, 1999) or the eyes are competing (Lee and Blake, 1999). Correspondingly, it has been

59   debated whether the visual competition is resolved at the monocular level or at the higher levels

60   in the visual processing hierarchy (Brascamp et al., 2018; Blake, 2022). This debate has settled

61   into hybrid models (for a review see Tong et al., 2006), where the recruitment of different brain

62   regions in rivalry depends on the type of stimuli and the specifics of their presentation.

63   He et al. (2005) noted that the eye vs stimulus rivalry debate ignored the fact that the

64   visual system operates in parallel streams, including the M and P pathways. They proposed BR

65   as a P pathway phenomenon, based on the psychophysical observations that there is more

66   complete suppression of P pathway stimuli than M pathway stimuli, as indicated by fewer

67   number of perceptual alternations and/or less piecemeal rivalry or fusion (Levelt, 1965, 1967;

68   O'Shea and Blake, 1986; Burke et al., 1999; Carlson and He, 2000). More direct psychophysical

69   investigation of the two pathways was performed by (Denison and Silver, 2012). Using an

70   interocular switch (IOS) rivalry paradigm, in which the rivalry stimuli were swapped between

71 eyes in every 1/3 seconds (Logothetis et al., 1996), they found that participants more frequently

72 experienced slow irregular perceptual alternations (i.e., stimulus rivalry) than fast regular

73 alternations (i.e., eye rivalry) using their P-tuned stimuli compared to M-tuned stimuli. This

74 suggested that the P pathway was more closely tied to perceptual resolution than the M pathway

75 (He et al., 2005). However, it is difficult to isolate the M and P pathways using different stimuli,

76 and this conclusion has not yet been tested directly by separately measuring the neural activity in

77 the M and P pathways during rivalry.

78   Two previous studies measured the human LGN activity during binocular rivalry, both

79 demonstrating the modulation of the LGN with perception (Haynes et al., 2005; Wunderlich et

80 al., 2005). We sought to replicate these studies and also eliminate a confound common to both.

81 These studies used colored stimuli and anaglyph glasses to stimulate each eye independently,

82 with no counterbalancing between eyes. For example, the rivalling stimuli used in (Wunderlich

83 et al., 2005) were red/green, which can be coded by single color-opponent neurons in the LGN.

84 We wanted to eliminate the possibility that the magnitude of rivalry measured in the LGN could

85 be confounded with color opponent mechanisms. We therefore used achromatic grating stimuli

86 in our study.

87   Our goal in this research was to directly measure the contributions of the M and P

88 pathways in conventional BR and in IOS rivalry, by measuring activity in the disjoint M and P

89 subdivisions of the LGN (Figure 1b). Using functional magnetic resonance imaging (fMRI), we

90 conducted both the conventional BR and the IOS paradigms using the same participants and

91 stimuli, two achromatic gratings rotating in opposite directions. We also compared these

92 activations to physically alternating stimuli with the same temporal sequence (i.e., replay).

93

94 **Materials and Methods**

95 **Participants**

96 The three participants for this study (1 male and 2 females, aged 28–33 years) were the same as

97 in Yildirim et al. (2022). They were compensated at a $20/hour rate for their participation. All

98 participants reported normal or corrected-to-normal vision. The participants used the generic

99 sighting tests to determine their dominant eye. S1 and S2 reported right eye dominance in

100 sighting while S3 reported left eye dominance. The protocols for this study and Yildirim et al.

101 (2022) were approved by the University of Delaware Institutional Review Board.

102

103 **Neuroimaging**

104 Three 90-minute sessions were conducted on three separate days. Participants were positioned in

105 a 3T Siemens Magnetom Prisma MRI scanner with a 64-channel head coil. At the beginning of

106 each session, we acquired a 3D MPRAGE sequence (0.7 mm isotropic voxels, repetition time

107 (TR) = 2080 ms, echo time (TE) = 4.64 ms, inversion time (TI) = 1050 ms, flip angle (α) = 9°,

108 field of view (FoV) = 210 mm, phase-encoding acceleration factor = 2, scan time approximately

109 6 min). All subsequent scans were aligned to this T1-weighted image of each subject and

110 analyzed in their native space (i.e., the T1- weighted image from their first session).

111 Whole brain fMRI data were acquired with a multi-band EPI sequence with 84

112 interleaved transversal slices (1.5 mm isotropic voxels, TR = 1500 ms, TE = 39 ms; α = 75°;

113 FoV = 192 mm, bandwidth = 1562 Hz/Px, phase encoding = A $\rightarrow$ P, slice acceleration factor =

114 6) which took 5 minutes. In each session, there were approximately ten 5-minute fMRI runs.

115

116 **Apparatus**

117 Stimuli for binocular rivalry experiments were presented with a ProPixx (VPixx, Inc.) projector

118 with a refresh rate of 120 Hz and 1920×1080 resolution. Participants wore circularly polarized

119 paper eyeglasses, and a synchronized circularly polarized filter was positioned in front of the

120 projector lens allowing for presenting different stimuli to each eye at 60 Hz. We measured

121 maximum 5% leakage between the left and right filters of the polarized glasses. The experiments

122 were controlled by a Linux computer and prepared in MATLAB, using the DataPixx toolbox for

123 the ProPixx projector, and Psychophysics Toolbox (Brainard, 1997; Pelli, 1997; Kleiner et al.,

124 2007) routines. Participants held a response box (fORPS, Cambridge Research Systems Ltd.) in

125 their right hand, with their index and middle fingers placed on separate buttons.

126

127 **Experimental Procedures**

128 During the 5-minute fMRI runs, the participants were instructed to fixate on the central dot in the

129 display, around which they were presented rotating gratings. The participants were experienced

130 with the experimental procedures, including keeping their eyes on the fixation dot, since S1 and

131 S3 participated in our pilot study and S2 had practiced inside MRI before their participation to

132 this study. Binocular rivalry usually manifests piecemeal over the large stimuli like we needed to

133 use to simulate a significant volume of the LGN and to minimize the effects of fixation errors,

134 but rotation has been shown to aid in the coherent perception of the full-field stimulus (Haynes et

135 al., 2005; Sylvester et al., 2007). Participants continuously reported the perceived rotation

136 throughout each run using a response box by pressing and holding the button under their index

137 finger to indicate counterclockwise rotation, the button under their middle finger to indicate

138 clockwise rotation, or both buttons simultaneously for a mixture perception. There were also six

139   5-s blank periods presented throughout a 5-minute run, during which the participants did not

140   press any buttons. These blank periods consisted of a blank neutral gray screen and were

141   pseudorandomly placed outside the first or last 30 s of the block and separated by at least 25 s of

142   visual stimuli.

143   A 5-minute run could be one of the three conditions: conventional rivalry, replay, or IOS

144   rivalry (see Figure 2). At the beginning of the first session, while the T1-weighted image of their

145   brain was obtained, participants completed a practice conventional rivalry run. The order of the

146   three conditions within a session was fit to a Latin-Square design and the starting condition was

147   counterbalanced between participants. However, some runs needed to be repeated due to errors

148   in video frame synchronizations that disrupted the dichoptic presentation and were replaced at

149   the end of the session or at the beginning of the participant's next session. Across all the

150   experimental sessions, there were 10 runs for each condition for each participant, with the

151   exception that there were nine rivalry and nine replay runs for S2 and eight IOS rivalry blocks

152   for S3.

153

154   ***Rivalry***

155   The conventional rivalry condition, hereafter simply referred to as "rivalry", is illustrated on the

156   left side of Figure 2. Each eye was presented with a grating rotating in opposite directions at $\omega =$

157   1 cycles/second. Each grating subtended 12° of visual angle in diameter and had a full-contrast

158   sinusoidal profile with a spatial frequency of 7 cycles/degree. Each grating was framed by a

159   black circle, measuring 12.5° in diameter to act as a binocular anchor, and was presented on a

160   neutral gray background. The luminance of the blank gray background with the polarization

161   shutter active on the projector was 260.6 cd/m^2 (PhotoResearch PR655) and 100.9 cd/m^2

162   measured through either side of the polarization filters that the subjects wore. The rotating

163   stimulus had a projected luminance of 262.7 cd/m^2, that is, the same as the neutral background.

164   Measured through one of the glasses, it was 70.46 cd/m^2. The clockwise and counterclockwise

165   gratings were counterbalanced between the eyes across rivalry runs, with the initial directions

166   also counterbalanced across participants.

167

168   *Replay*

169   Replay was a control condition for the conventional rivalry. The participant's reports from a

170   previous rivalry run were used to mimic their perception. For the first replay run, the perceptual

171   reports from the practice rivalry run were used. This was because of the Latin-square design for

172   the order of the conditions where the first replay run was not always preceded by a conventional

173   rivalry run. As illustrated in Figure 2 for replay, to mimic the participant's clockwise perception

174   in rivalry, the clockwise rotating grating was presented to the corresponding eye while the other

175   eye was presented with the blank instead of a grating. Similarly, if the participant reported

176   counterclockwise rotation in rivalry, then the counterclockwise rotating grating was shown to the

177   matching eye while the other eye was presented with the blank in replay. For the reports of

178   mixture perception in rivalry, the two rotations, superimposed on each other at 50% opacity,

179   were shown to both eyes in replay. The blank screen periods in replay were also matched to the

180   rivalry run.

181

182   *Interocular Switch (IOS) Rivalry*

183   The IOS rivalry runs followed the same procedure as the rivalry runs, with the addition of

184   interocular switches of the stimuli (see Figure 2). In the literature, IOS rivalry paradigms used

185   stable orthogonal gratings that flickered at a high frequency (e.g., 18 Hz) and swapped between

186   eyes three times per second (Logothetis et al., 1996; Denison and Silver, 2012). For the current

187   study, we found that flickering the rotating stimuli drastically impaired the perception of

188   rotation; therefore, the stimuli in our IOS rivalry experiments did not flicker but their rotation did

189   present a temporal modulation. The eye swap intervals of the stimuli were determined with the

190   following constraints. First, the swap interval had to be greater than 1 s, the time for a 360°

191   rotation, to allow a stable perception long enough for the participants to respond. Second, the

192   swaps were constrained to occur irregularly to prevent a dull plaid perception of rotations,

193   always touching each other at the same point and rotating backwards at regular intervals.

194   Therefore, the gratings in the IOS rivalry runs swapped between eyes at times randomly chosen

195   between 2.5–3.5 s.

196

197   **Data Processing and Analyses**

198   We used FSL software (https://fsl.fmrib.ox.ac.uk/fsl/fslwiki/FSL) to process all MRI data unless

199   otherwise noted. Functional data were pre-processed using motion correction via MCFLIRT,

200   intensity normalization, high-pass temporal filtering, and no spatial smoothing.

201   The fMRI data for each rivalry and replay block were analyzed with a generalized linear

202   model (GLM). Two explanatory variables (EVs), LE perception and RE perception, were

203   defined based on the participant's perceptual reports. Mixture perceptions were included in both

204   EVs, and the random blank screens were excluded. Motion outlier volumes, identified with the

205   fsl_motion_outliers command thresholded at the 75th percentile + 1.5 times the interquartile

206   range, were added as a confound. All the possible contrasts were computed between the two

207   EVs. A fixed-effects analysis was used for each participant to combine the multiple scanning

208   runs for each of the rivalry and replay conditions, with all the possible contrasts computed

209   between the conditions. The significance threshold was not corrected for multiple comparisons

210   as the analysis was only performed in the LGN. A suppression index (SI) for each voxel was

211   calculated using the B weights provided by the GLM: SI $= B_{\text{rivalry}-\text{replay}}/B_{\text{replay}+\text{rivalry}}$, where

212    $B_{\text{rivalry}-\text{replay}}$ is the contrast between the rivalry and replay runs, and $B_{\text{replay}+\text{rivalry}}$ is their

213   conjunction. An index of 0 would indicate complete suppression during rivalry, wherein voxels

214   would exhibit similar amplitudes to those induced by the physical stimulus alternations in replay,

215   whereas a significantly positive index would indicate that voxels in the LGN were still activated

216   by the non-perceived stimuli.

217   The fMRI data for the IOS rivalry condition were not processed, as stimulus rivalry was

218   not observed in any participant (see Results).

219

220   ***Regions of Interest (ROI) Analyses***

221   The ROI in this study were the M and P regions and the eye-specific regions in the LGN. For the

222   M and P comparisons, the LGN were anatomically identified for each participant separately

223   using quantitative MRI and the M and P regions in each LGN were segregated based on their

224   difference in T1 relaxation time, which was reported in Yildirim et al. (2022). For the eye-

225   specific region comparisons, the anatomically identified LGN were adjusted for the visually

226   active areas using a visual hemifield stimulation. The contralateral (CL) and the ipsilateral (IL)

227   eye regions were then segregated based on their responses to the eye-specific visual stimulation

228   in both monocular and dichoptic viewing conditions. Eye-specific voxels were determined as

229   those that exhibited a significant contrast between eyes in the combined GLM analysis of the

230   monocular and dichoptic eye localizers, as detailed in Yildirim et al. (2022).

231   The GLM results for the rivalry–replay contrast were inspected in the M and P sections

232 of each LGN, and the suppression index was compared between the regions. In addition, an

233 event-related averaged time series was computed in MATLAB. For each of the eye-specific

234 voxels in each LGN (see Figure S1 of Yildirim et al., 2022), the preprocessed fMRI data were

235 converted to percent change using the mean baseline activity, corresponded to the blank screens,

236 corrected 6 s for the hemodynamic delay. The data were then upsampled in time to 100 ms

237 resolution (from the original TR of 1.5 s). For each event, corresponding to a participant's

238 indication of a single rotation direction, the event-related average was calculated between 5 s

239 before and 15 s after the participant's initial response. This analysis was carried for the eye-

240 specific regions in the LGN but not separately for those in the M and P because the contralateral

241 M layer could not be identified by the eye localizer tasks (see Figure S1 of Yildirim et al., 2022).

242

243   **Results**

244 **Perceptual Findings**

245 We calculated the durations of unmixed perception of a single rotation, corresponding to a single

246 eye, based on the participants' perceptual reports. These are shown in Figure 3, for perceptions

247 lasted more than 2 s, concatenated across all scanning runs for the rivalry conditions. As

248 designed, the rivalry and the replay conditions resulted in similar perceptual reports, since the

249 replay stimuli were constructed to mimic the perception of the rivalrous stimuli. The average

250 unmixed perception during rivalry across participants was around 7 s, means ranging from 4.45 s

251 to 8.81 s, and the average median was 5.77, medians ranging from 3.83 to 7.96 (black lines for

252 rivalry in Figure 3). The durations of the perceived clockwise vs counterclockwise rotations did

253 not differ for any participant during rivalry. However, RE perceptions were longer than LE

254   perceptions for two of the three participants, $t(257) = 4.12$, $p_{Bonf} < .001$, $d = .52$ for S2 and $t(292)$

255    $= 4.23$, $p_{Bonf} < .001$, $d = .49$ for S3. During IOS rivalry, on the other hand, one of these

256   participants (S2) experienced longer LE perceptions instead, $t(551) = 3.46$, $p_{Bonf} = .002$, $d = .31$,

257   and the other participant (S3) experienced longer clockwise perceptions ($M = 2.59$, $SD = .37$)

258   compared to the counterclockwise perceptions ($M = 2.48$, $SD = .35$), $t(272) = 2.43$, $p_{Bonf} = .047$, d

259    $= .29$.

260   As can be seen in the third column in Figure 3, the perceptual reports demonstrated no

261   stimulus rivalry in the IOS condition. Neither the number of occurrences of exclusive

262   perceptions (y-axis) nor the perceptual durations (the distribution and the black lines) during IOS

263   rivalry were similar to the rivalry condition. In fact, the perception was failed to be resolved on a

264   single rotation, or on a single eye, during IOS rivalry. To quantify the amount of eye rivalry,

265   stimulus rivalry, and the mixture perception, we focused on when the interocular switch (i.e.,

266   eye-swap) of the stimuli occurred. If the eye swap went unnoticed, indicated by the exclusive

267   perception of a rotation by the time the swap had happened, we counted it as stimulus rivalry. On

268   the other hand, if the eye swap was noticed, indicated by the initiation of an exclusive perception

269   following the eye swap within 500 ms, we counted it as eye rivalry. There was neither eye

270   rivalry nor stimulus rivalry, instead, the reported perception was mostly the mixture of the two

271   rotations for the vast majority of the eye swaps, 99.57% for S1, 99.68% for S2, and 100% for S3.

272   Given our failure to induce IOS rivalry, the data for this experiment were not analyzed further.

273

274   **Rivalry in the M and P Regions of LGN**

275   The contrasts between the rivalry and replay conditions were examined with a GLM within each

276   LGN. As indicated by the z-scores for the rivalry–replay contrast in Figure 4a, rivalry and replay

277   activated similar number of voxels within each LGN and their M and P regions. There were

278   small number of voxels that were significantly more active during rivalry (white voxels) or

279   during replay (black voxels). As can be seen in Figure 4a, these significant voxels were spread

280   evenly across the M (area below the red line) and the P regions (area above the red line).

281   However, the distribution of rivalry- and replay-related activity in the LGN looked similar to the

282   retinotopic map in LGN, representing the visual eccentricity. That is, replay (blue areas in Figure

283   4a) activated regions representing the central field whereas rivalry (yellow areas in Figure 4a)

284   activated regions representing the surround field (but see Discussion).

285   In addition, there were similar levels of overall suppression in each LGN, demonstrated

286   by the suppression indices around 0 (see Figure 4b), i.e., the unperceived stimuli did not increase

287   activity in the LGN, whether it was present (in the rivalry condition) or not (in the replay

288   condition). We conducted a Bayesian one sample t-test for each LGN and the M and P divisions

289   to see the likelihood of data favoring the null distribution (i.e., index not different than 0,

290   indicating successful suppression) over the alternative distribution (i.e., index different than 0).

291   The odds were in favor of the null hypothesis at least moderately across all LGN, $BF01$'s > 8 for

292   LGN, $BF01$'s > 5.5 for P regions, and $BF01$'s > 5 for five out of six M regions. The only ROI

293   that the Bayesian factor favored the alternative hypothesis was S2 right LGN's M section, $BF10$

294   = 11.8. The suppression index was positive in this M section, indicating higher relative activation

295   during rivalry and thus incomplete suppression (see Figure 4b). Last, a Bayesian independent

296   samples t-test was employed on the indices to find how likely the data supports the alternative

297   hypothesis that the suppression index is different in the M and P sections of the LGN over the

298   null hypothesis of no difference. Bayesian factors revealed that the odds were moderately in

299   favor of the null hypothesis, *BF01*'s > 3.5 for all LGN, indicating similar levels of suppression in

300   the M and P sections.

301

302   **Rivalry in the Eye-specific Regions of LGN**

303   The event-related averages of the contralateral (CL) and ipsilateral (IL) voxels in each LGN,

304   registered to the beginning of the participants' report of stable perception (with durations $\geq$ 6 s,

305   i.e., four TRs of 1.5 s each), are shown in Figure 5. We examined the differences in signal for the

306   CL eye voxels (blue line) and the IL eye voxels (red line), indicating that the CL (IL,

307   respectively) voxels showed increased activity following the perceptual resolution on the CL (IL)

308   eye while showing suppressed activity following the perceptual resolution on the IL (CL) eye.

309   As can be seen in Figure 5, rivalry and replay conditions did not yield similar results. The

310   rivalry condition resulted in more separable oscillations of eye-specific voxels for three LGN (S1

311   right LGN, S3 left and right LGN), all of which were also more reliable in their eye-specific

312   region analysis as reported in (Yildirim et al., 2022). Focusing only on these LGN in Figure 5,

313   the oscillations demonstrated signs of the exclusive perception earlier and longer for the rivalry

314   than the replay condition. The LGN that had few numbers of significant eye-specific voxels (S1

315   left LGN and S2 right LGN, see (Yildirim et al., 2022) showed more variance, as evident by the

316   larger 95% confidence intervals (CIs) in the figure.

317

318   **Discussion**

319   We measured the relative activities of the M and P pathways in the human LGN during binocular

320   rivalry to test the predictions that they might differ (He et al., 2005; Denison and Silver, 2012).

321   Using fMRI, we observed similar overall responses in the disjoint M and P layers to perceptual

322   alternations induced by rivalry or replay, failing to support this hypothesis. By using polarizing

323   filters to present achromatic stimuli dichoptically, we also confirmed that binocular rivalry can

324   be observed in the human LGN and is not simply an artifact of color opponent processes. As

325   discussed in Yildirim et al. (2022), the contralateral M layer did not appear reliably; therefore,

326   the comparison of M and P was made in overall activity but not in the time series activity. Our

327   attempts to induce rivalry in the IOS paradigm was unsuccessful using our stimuli, and we were

328   therefore unable to test whether stimulus rivalry was associated with the P but not M pathway

329   (Denison and Silver, 2012).

330   We used stimuli that did not specifically bias M or P neurons so that any differential

331   activity between them is not due to stimulus and found similar activations during rivalry and

332   replay for the M and P layers of LGN. However, we did observe a distribution of rivalry- and

333   replay-related activity in the LGN (Figure 4a) that resembled the retinotopic map in LGN

334   representing the visual eccentricity (Schneider et al., 2004; DeSimone et al., 2015), such that

335   replay activated areas that corresponded to central field and rivalry activated areas that

336   corresponded to the surround field of the stimulus. One possible explanation could be that eye

337   movements with participants being cross-eyed during rivalry could cause changes in peripheral

338   activation. However, this is unlikely, as our experienced participants were trained to fixate and

339   our stimuli were full-field, which by design are less susceptible to small changes in fixation.

340   Another explanation for the potential retinotopic pattern could be the difference in the piecemeal

341   perception induced by rivalry and replay. The large rivalry stimuli might have resulted in

342   different rotations at center and surround, reported as a mixture perception by the participants,

343   whereas the corresponding replay stimulus was homogeneous and weaker because the rotations

344   were superimposed at half opacity. However, we did not localize the retinotopic maps with an

345   eccentricity manipulation in the visual stimulus; thus, any conclusion requires additional

346   research.

347   Using rotation-opponent achromatic gratings, we observed eye-specific responses to the

348   exclusive eye perceptions that were not as pronounced or prolonged compared to those in

349   Haynes et al. (2005). They used orthogonal blue/red gratings rotating in the same direction. It is

350   possible that rivalry between constantly orthogonal gratings supported longer perceptions (Blake

351   et al., 2003), whereas the motion opponency in our study prevented building coherent perception.

352   In our stimuli, the gratings were only briefly orthogonal as they rotated in opposite directions,

353   and thus their rivalry was not based on spatial orthogonality. The mean duration of the exclusive

354   perception in our study was approximately 2 s shorter. However, Haynes et al. (2005) did not

355   give an option to report mixture perception, so it is difficult to compare with our study precisely.

356   We found in some participants that the perceptual reports during rivalry occurred earlier

357   than during replay. This would be consistent with Wunderlich et al. (2005) and might reflect the

358   build-up activity in the monocular neurons preceding perceptual resolution (Wolfe, 1986; Lehky,

359   1988; Blake, 1989; Tong, 2001). Surprisingly, the eye-specific activity in the replay condition

360   was noisier than during the rivalry condition. We speculate that this could be driven by factors

361   such as reaction time noise or motion adaptation and the resulting motion after-effects during

362   replay. Also, the monocular neurons in the LGN receive binocular feedback from V1 (Dougherty

363   et al., 2021) and fMRI measurements may have different confounds in the two conditions

364   through feedback and lateral connections (Dougherty et al., 2019). During rivalry, for example, it

365   might be the feedback information that is being suppressed. Unperceived information could still

366   be transmitted feedforward, but the feedback activity would be required for conscious perception

367   (Pascual-Leone and Walsh, 2001). This could also explain previous findings indicating

368   sensitivity to the changes in the suppressed stimulus' even if it might be reduced (e.g., Wales and

369   Fox, 1970).

370   We observed that two out of three participants showed a RE dominance during rivalry, as

371   indicated by the longer exclusive perceptions for the RE than the LE. These participants reported

372   having different dominant eyes in the simple sighting tests. Correlations between the dominant

373   eye in sighting and the dominant eye in perception during rivalry have been reported previously

374   (Porac and Coren, 1978; Handa et al., 2004); however, it has been also suggested that BR is

375   sensitive to the sensory eye dominance and not sighting eye dominance (Dieter et al., 2017). Our

376   results, albeit with a small sample, supports this latter conclusion.

377   When the rotating gratings swapped between eyes during the IOS rivalry experiment,

378   mixture perceptions dominated. Given that neither stimulus dominated, this suggests that both

379   stimulus and eye competition occurred. Previous research with the IOS paradigm used

380   orthogonal gratings that rapidly swapped between eyes while also flickering rapidly to mask the

381   eye swap. This results in more stimulus than eye rivalry (Logothetis et al., 1996; Lee and Blake,

382   1999; Silver and Logothetis, 2007; Bhardwaj and O'Shea, 2012; Denison and Silver, 2012; Patel

383   et al., 2015). Christiansen et al. (2017) found that the IOS rivalry stimuli that differed only in

384   color resulted in stimulus rivalry whereas stimuli that differed in luminance did not. This is

385   consistent with our finding of no stimulus rivalry using the achromatic stimuli in our study. This

386   also suggests that the M-stimuli might not be optimal for generating slow stimulus alternations

387   (He et al., 2005; Denison and Silver, 2012).

388   Sandberg et al. (2011) used an eye-swapping procedure with flickering stimuli and found

389   that continuous perception was not disrupted by the eye swaps between the complex stimuli (i.e.,

390   faces/houses) but was for simple stimuli (i.e., orthogonal gratings, not rotating). This was the

391   case even when they scrambled their complex stimuli, suggesting an importance for overlapping

392   low-level features. Our rotating stimuli that continually changed the overlapping features may

393   therefore not be optimal to resolve the competition with the eye-swapping procedure.

394   In conclusion, this study demonstrated that binocular rivalry could be observed in the

395   human LGN using achromatic rotation-opponent rivalry stimuli. We observed nearly complete

396   suppression of the non-perceived eye activity in both the M and P regions, and a different time

397   course of activity between rivalry and the actual physical alternation of the different stimuli,

398   despite similar perceptual experiences.

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488

489

490   **Figure Legends**

491   **Figure 1.** *The Structure of Lateral Geniculate Nucleus.* C = Contralateral eye, I = Ipsilateral eye,

492   M = Magnocellular, P = Parvocellular. Tracings were generated based on Andrews et al. (1997).

493

494   **Figure 2.** *The Stimulus Presentation for the Experimental Conditions.* Rivalry was the

495   conventional binocular rivalry paradigm in which each eye was presented with a different

496   stimulus, rotations counterbalanced across the eyes in the actual experiment. Replay was the

497   physical alternations of the stimuli matching with the perceptual reports of the observer during a

498   previous rivalry block. IOS Rivalry was the interocular switch paradigm in which the rivalry

499   stimuli swapped between the eyes in every few seconds, randomly chosen between 2.5-3.5 s.

500

501   **Figure 3.** *Histograms for Durations of Exclusive Perceptions during Rivalry.* Riv: Rivalry, IOS:

502   interocular switch rivalry, CW: clockwise rotation, -CW: counterclockwise rotation. On the third

503   column are the histograms collapsed across the two rotations for exclusive perceptions. Black

504   lines reflect the median duration. Bin interval is 1 s.

505

506   **Figure 4.** *GLM Results for Rivalry and Replay in the M and P Regions of LGN.* **a)** Coronal slices

507   of each LGN showing the z-scores for the rivalry−replay contrast. The red line delimits the

508   boundary between the M and P regions according to their T1 relaxation time (Yildirim et al.,

509   2022). *$p < .05$, uncorrected for multiple comparisons for voxels. **b)** Scatterplots of the M and P

510   voxels, indicated by their T1 relaxation time in seconds on the x-axis, showing similar

511   suppression for rivalry and replay. The suppression index on the y-axis was calculated by the *B*

512   weights. For illustration purposes, the voxels with indices beyond 10 and −10 were plotted at 10

513 and −10 respectively. Black lines indicate the mean suppression indices for the M and P voxels.

514 Error bars are the SEM. **p = .02, Bonferroni corrected for six LGN.

515

516 **Figure 5.** *fMRI Activity around the Exclusive Eye Perceptions during Rivalry and Replay*. The *x*-

517 axis shows the time around when the stable perception started (time 0), indicated by the

518 participant's perceptual reports. The *y*-axis shows the difference in the percent fMRI signal for

519 the contralateral (CL) eye perceptions vs ipsilateral (IL) eye perceptions. Error shades are 95%

520 CIs. *p < .05

Rivalry

Left Eye   Right Eye

Replay

Left Eye   Right Eye

For anticlockwise perception in rivalry

For clockwise perception in rivalry

For piecemeal perception in rivalry

IOS Rivalry

Left Eye

Right Eye

2.5 - 3.5 s

time