1

Dependence of perceptual saccadic suppression on peri-saccadic image flow properties and luminance contrast polarity

5

Matthias P. Baumann[1,2], Saad Idrees[1],
Thomas A Münch[1], and Ziad M. Hafed[1,2]

1. Werner Reichardt Centre for Integrative Neuroscience, Tübingen University, Tübingen, Germany
2. Hertie Institute for Clinical Brain Research, Tübingen University, Tübingen, Germany

12

13

Correspondence to:

Matthias P. Baumann (matthias-philipp.baumann@student.uni-tuebingen.de)

16

21

22

23   **Abstract**

24

25   Across saccades, perceptual detectability of brief visual stimuli is strongly diminished.

26   We recently observed that this perceptual suppression phenomenon is jumpstarted in

27   the retina, suggesting that the phenomenon might be significantly more visual in

28   nature than normally acknowledged. Here, we explicitly compared saccadic

29   suppression strength when saccades were made across a uniform image of constant

30   luminance versus when saccades were made across image patches of different

31   luminance, width, and trans-saccadic luminance polarity. We measured perceptual

32   contrast thresholds of human subjects for brief peri-saccadic flashes of positive

33   (luminance increments) or negative (luminance decrements) polarity. Perceptual

34   thresholds were >6-7 times higher when saccades translated a luminance stripe or

35   edge across the retina than when saccades were made over a completely uniform

36   image patch. Critically, both background luminance and flash luminance polarity

37   relative to the background strongly modulated peri-saccadic contrast thresholds. In

38   addition, all of these very same visual dependencies also occurred in the absence of

39   any saccades, but with qualitatively similar rapid translations of image patches

40   across the retina. Our results support the notion that perceptual saccadic

41   suppression may be fundamentally a visual phenomenon, and they motivate

42   neurophysiological and theoretical investigations on the role of saccadic eye

43   movement commands in modulating its properties.

44

45

46

47   **Keywords**

48

51

52

53   **Introduction**

54

55   Due to their ballistic nature, visual input across saccades invariably includes periods

56   of large image uncertainty. Perceptual cancelation during such periods takes place,

57   resulting in a seamless subjective visual experience despite the occurrence of

58   saccades as often as several times in just one second (Melcher, 2011; Wurtz, 2008;

59   Wurtz, Joiner, & Berman, 2011; Zimmermann & Bremmer, 2016). In the laboratory,

60   the properties of peri-saccadic vision have been studied by presenting very brief and

61   fleeting "probe" stimuli around the time of saccadic eye movements. Such stimuli act

62   as impulses that essentially capture the instantaneous and momentary state of the

63   visual system (Matin, 1974; Ross, Morrone, Goldberg, & Burr, 2001).

64

65   When presenting very brief peri-saccadic visual stimuli, a prominent observation is a

66   massive, but transient, suppression of visual sensitivity. In this striking phenomenon,

67   a visual probe goes completely unnoticed if presented within approximately +/- 50 ms

68   from saccade onset, even if it would be detected effortlessly when presented under

69   fixation (Beeler, 1967; Brooks & Fuchs, 1975; Idrees, Baumann, Franke, Munch, &

70   Hafed, 2020; Latour, 1962). This phenomenon was labeled saccadic suppression

71   (Zuber & Stark, 1966), and it has attracted investigation by vision scientists for many

72   decades (Binda & Morrone, 2018; Castet, Jeanjean, & Masson, 2001; Castet &

73   Masson, 2000; Matin, 1974; Schweitzer & Rolfs, 2020; Wurtz, 2008). Saccadic

74   suppression is robust, and it occurs for both reflexive and deliberate saccades

75   (Gremmler & Lappe, 2017). It also seems to occur for saccades of all sizes, including

76   microsaccades (Beeler, 1967; Chen & Hafed, 2017; Hafed & Krauzlis, 2010; Zuber &

77   Stark, 1966), and it even acts to shape the long term dynamics of visual sensitivity

78   well after the eye movements (J. Bellet, Chen, & Hafed, 2017; Benedetto & Morrone,

79   2017). Most interestingly, neural responses to visual probes in a variety of brain

80   areas are also suppressed if the probes occur peri-saccadically (Berman,

81   Cavanaugh, McAlonan, & Wurtz, 2017; Bremmer, Kubischik, Hoffmann, &

82   Krekelberg, 2009; Chen & Hafed, 2017; Chen, Ignashchenkova, Thier, & Hafed,

83   2015; Hafed & Krauzlis, 2010; Idrees, Baumann, Franke, et al., 2020; Idrees,

84   Baumann, Korympidou, et al., 2020; Kagan, Gur, & Snodderly, 2008; Reppas, Usrey,

85   & Reid, 2002; Robinson & Wurtz, 1976).

86

87   For perhaps as long as saccadic suppression has been investigated, there have

88   been debates on its origins. On the one hand, according to the "active hypothesis", it

89   has been suggested that suppression relies on knowledge of saccade generation

90   commands to actively suppress visual sensitivity, through efference copies or

91   corollary discharge from (pre-) motor areas (Beeler, 1967; Diamond, Ross, &

92   Morrone, 2000; Duffy & Lombroso, 1968; Zuber & Stark, 1966). Perceptually, a

93   showpiece for this hypothesis was the observation that saccadic suppression can be

94   selective (Burr, Morrone, & Ross, 1994): brief flashes of low spatial frequency

95   patterns are suppressed much more than brief flashes of high spatial frequency

96   patterns (Burr et al., 1994). This observation was interpreted as evidence for an

97   active movement-related signal specifically targeting the magnocellular visual

98   pathway, which is sensitive to low spatial frequencies (DeYoe & Van Essen, 1988;

99   Merigan & Maunsell, 1993). On the other hand, according to the "visual hypothesis",

100   it is the visual consequences of saccades that jumpstart suppression. This is

101   supported by the observation that brief probe flashes near the onset of global image

102   translations (similar to those caused by saccades) are also perceptually suppressed

103   (Adey & Noda, 1973; Brooks & Fuchs, 1975; Brooks, Impelman, & Lum, 1981; Castet

104   et al., 2001; Diamond et al., 2000; Idrees, Baumann, Franke, et al., 2020; Mackay,

105   1970; Mitrani, Mateeff, & Yakimoff, 1971; Mitrani, Radil-Weiss, Yakimoff, Mateeff, &

106   Bozkov, 1975; Mitrani, Yakimoff, & Mateeff, 1973; Noda & Adey, 1974; Yakimoff,

107   Mitrani, & Mateeff, 1974). Recently, we also found that even selective suppression of

108   low spatial frequency patterns may be entirely visual in origin: both selective and

109   unselective suppression can happen with or without saccades, simply as a function

110   of visual context (Idrees, Baumann, Franke, et al., 2020). A key observation was that

111   saccade-like image translations activate, rather than suppress, the retinal image

112   processing cascade and result in afferent activity bursts in retinal ganglion cells;

113   responses to subsequent flashes are, in turn, suppressed through retinal-circuit (and

114   downstream) visual interactions (Idrees, Baumann, Franke, et al., 2020; Idrees,

115   Baumann, Korympidou, et al., 2020). Thus, from a visual perspective, perceptual

116   saccadic suppression involves visual-visual interactions between two kinds of

117   signals: (1) the visual consequences of saccadic eyeball rotations; and (2) the visual

118   consequences of flash onsets (Idrees, Baumann, Franke, et al., 2020).

119

4

120   Here, we explored these visual-visual interactions in more detail at the perceptual

121   level. We varied the image conditions across which gaze translated during saccades,

122   and we also tested image translations in the absence of saccades. We additionally

123   explored influences of flash polarity (luminance increments or decrements relative to

124   the background), motivated by quantitative differences between ON and OFF retinal

125   pathways in saccadic suppression (Idrees, Baumann, Korympidou, et al., 2020). We

126   found that saccadic suppression exhibits a large diversity of visual dependencies,

127   which also emerge with image translations in the absence of saccades. Our results

128   strongly motivate revisiting both the movement-related and visual components of

129   saccadic suppression, and investigating how saccade movement commands may

130   interact with visual-visual interactions in shaping trans-saccadic visual perception.

131

132

133 **Methods**

134

135

136 *Subjects and ethical approvals*

137 We collected data from 6 human subjects (3 females) who provided informed

138 consent. Two subjects were authors of this study (MPB and SI), and the others were

139 naïve to the purposes of the experiments. The subjects' ages were in the range of

140 22-32 years, and the subjects were compensated 10 euros per session of

141 approximately 60 minutes each. Each subject's data were collected across 10

142 individual sessions, resulting in 60 sessions in total. The experiments were approved

143 by ethics committees at the Medical Faculty of Tübingen University, and they were in

144 accordance with the Declaration of Helsinki.

145

146

147 *Laboratory setup*

148 The laboratory setup was similar to that described in recent studies from our group

149 (Bogadhi, Buonocore, & Hafed, 2020; Idrees, Baumann, Franke, et al., 2020).

150 Subjects sat in front of a CRT display placed 57 cm in front of their eyes, and the

151 display had a resolution of 41 pixels/deg and a refresh rate of 85 Hz. In visual angles,

152 the display spanned approximately 34 deg horizontally and 26 deg vertically. We

153 stabilized subjects' heads in front of the display using a custom-built device,

154 consisting of a chin rest, forehead rest, temple guides and a head-band (Hafed,

155 2013). In addition, we tracked eye movements using a video-based eye tracker

156 (Eyelink 1000, SR Research Ltd, Canada) that was placed on the desktop under the

157 display and aimed at the left eye. Before running the experiments, we linearized the

158 display (8-bit resolution), such that we had equal steps of luminance increments or

159 decrements (relative to the background luminance) for the different experimental

160 variants (Idrees, Baumann, Franke, et al., 2020). All experiments were controlled

161 using the Psychophysics Toolbox (Brainard, 1997; Kleiner, Brainard, & Pelli, 2007;

162 Pelli, 1997), which also synchronized data from the eye tracker using Eyelink

163 extensions of the toolbox (Cornelissen, Peters, & Palmer, 2002). Data and events

164 were stored and later analyzed using Matlab.

165

166

167 *Experimental procedures*

168 Our general approach was to present a brief probe flash (1 display frame;

169 approximately 12 ms) at a specific time relative to a visual transient. In some

170 conditions, such a visual transient was caused by a real saccade shifting the retinal

171 image globally. In other conditions, it was caused by either a luminance step in the

172 display during fixation or by a transient translation of the display image (to simulate a

173 saccade-like image displacement). The brief probe was presented at one of multiple

174 possible display locations, which were fixed in position on the display for all

175 experiments. Subjects had to identify, on every trial, at which of the locations the

176 probe flash appeared. Therefore, the experiment utilized a multiple-alternative forced

177 choice design. If subjects experienced suppression of their perceptual sensitivity,

178 then their proportion of correct responses was expected to significantly decrease

179 relative to normal perceptual performance.

180

181 To obtain a sensitive measure of perceptual sensitivity across the different

182 conditions, we varied the flash contrast (luminance amplitude, either as an increment

183 or decrement from background luminance) across all trials, and we collected full

184 psychometric curves of perceptual detectability. This provided a much more sensitive

185 way of assessing perceptual thresholds across conditions when compared to just

186 plotting the percentage of correct trials for just one flash contrast (Idrees, Baumann,

187 Franke, et al., 2020).

188

189 Across ten sessions per subject, we tested 5 different visual transient conditions,

190 along with two different background luminance conditions at the time of perceptual

191 discrimination (i.e. at the time of probe flash occurrence). We describe these

192 conditions in detail next. Each condition was tested separately in two sessions per

193 subject.

194

195 *(1) Real saccades across a uniform background:* In this condition, subjects started by

196 fixating a white fixation spot that appeared at 11.8 deg eccentricity from display

197 center, and located either to the right or left of display center as follows: 11.2 deg to

198 the right and either 3.8 deg above or below display center; or 11.2 deg to the left and

199 either 3.8 deg above or below display center (Fig. 1A, top). The fixation spot was a

200 square of 7.3 by 7.3 min arc size and 142.8 cd/m^2 luminance (Idrees, Baumann,

7

201 Franke, et al., 2020). After a random delay of 800-1700 ms after initial fixation spot

202 appearance, the fixation spot disappeared, and it simultaneously re-appeared at

203 display center. This was the instruction to generate a saccade towards the new spot

204 location (Fig. 1A, top). We then initiated an automatic program to detect saccade

205 onset. This program was described previously (Chen & Hafed, 2013), and it was also

206 similar to what we used recently in a similar context to the present one (Idrees,

207 Baumann, Franke, et al., 2020). Briefly, this saccade detection program collected a

208 recent history of eye position samples and used those to obtain a running estimate of

209 eye speed. If such speed exceeded a threshold, a saccade was detected. Upon

210 saccade detection, we presented a single-frame probe flash as the perceptual

211 discrimination stimulus (Fig. 1A, top). The probe flash occurred after one of 4

212 possible time points after online saccade detection: 24, 35, 47, or 59 ms. These time

213 points were guided by our experience in a similar context (Idrees, Baumann, Franke,

214 et al., 2020), and they allowed us to obtain a time course of recovery in perceptual

215 sensitivity after the saccades.
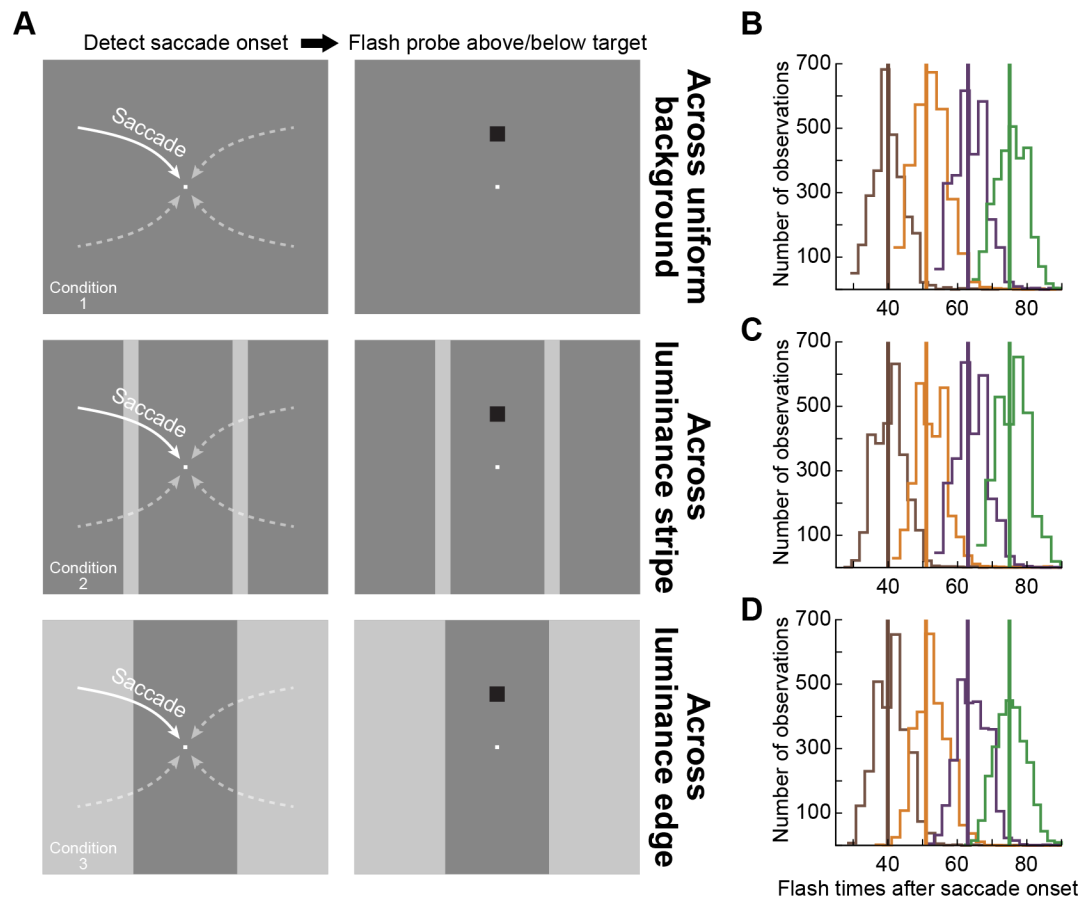
216

217

218

219

Figure 1 The different saccade conditions tested in our study. (A) Subjects made approximately 11.8 deg saccades towards display center from one of four possible locations. The saccades (schematized as curved arrows) were predominantly horizontal (see text), and we detected their onset online using a velocity criterion. Upon saccade detection, we presented a brief luminance flash at 7 deg either above or below the saccade target (right column of images). The flash was presented at one of four different delays from online saccade detection (see **B-D**). In condition 1 (top row), the saccades were made over a uniform background. In condition 2 (middle row), gaze crossed a vertical luminance stripe. And, in condition 3 (bottom row), the saccades brought gaze across a vertical luminance edge. We varied background luminance or the combination of pre- and post-saccadic background luminances across trials, and the probe flashes could also be of either positive (luminance increments relative to the background) or negative (luminance decrements) polarity. **(B)** After detecting saccades offline, we plotted the distributions of flash times collected during the experiments in condition 1 across all subjects. Our experimental manipulation succeeded in probing multiple times of perceptual sensitivity after saccade onset. The jitter in the individual distributions was due to variability in online saccade detection, as well as display update timing variability (due to the asynchrony between saccades and display refresh clocks). **(C, D)** Similar distributions of flash times for conditions 2 and 3, suggesting that differences in perceptual thresholds across conditions (see Results) were not attributable to different flash times relative to saccade onset. The thick vertical lines in **B-D** show the global average flash times for each colored distribution across all conditions.

Note that in all experimental conditions in which we used online saccade detection, we re-detected saccades offline in post-hoc analyses. This was because we could now refine saccade detection with an ability to look both forward and backward in

9

247   time during offline analyses (Chen & Hafed, 2013); see the data analysis section

248   below for further details. Across all experimental conditions with saccades being

249   detected online, we confirmed that the 4 probe flash times designated above were

250   occurring at 39.53 +/- 0.81, 51.38 +/- 0.85, 63.05 +/- 0.97, or 74.83 +/- 0.85 ms

251   (mean value +/- s.e.m. across all trials from all subjects) after saccade onset (Fig.

252   1B-D shows the distributions of flash times in this and the two other saccade

253   conditions described below). This was similar to the approach that we recently used

254   (Idrees, Baumann, Franke, et al., 2020). Moreover, we confirmed that flash times

255   after saccade onset were similar across all conditions employing real saccades (see

256   raw distributions in Fig. 1B-D); this way, we could safely conclude that differences in

257   the strength of perceptual saccadic suppression across the different conditions (see

258   Results) could not be attributed to systematic differences in the flash times after

259   saccades.

260

261   It should also be noted that with this approach of online saccade detection, we did

262   not present flashes pre-saccadically. This was a conscious choice given the large

263   numbers of trials needed in all of our experiments to collect full psychometric curves

264   at each flash time and for each background luminance and for each of either saccade

265   or fixation conditions. This is a strategy that we had also used in our recent

266   experiments (Idrees, Baumann, Franke, et al., 2020). However, in other conditions

267   described below (conditions 4 and 5), we did present flashes before visual transients,

268   confirming that "pre-saccadic" suppression does occur (in an expected manner), and

269   that it is consistent with all of our previously described results motivating the current

270   study (J. Bellet et al., 2017; Chen & Hafed, 2017; Hafed & Krauzlis, 2010; Idrees,

271   Baumann, Franke, et al., 2020).

272

273   The probe flash that was presented at different times after online saccade detection

274   was a square of 2.4 by 2.4 deg dimensions (Idrees, Baumann, Franke, et al., 2020).

275   In the current experiments, its luminance consisted of either a decrement (shown in

276   the examples of Fig. 1A) or increment relative to the background luminance, allowing

277   us to explore the impact of stimulus polarity on peri-saccadic perceptual sensitivity.

278   The background luminance itself was either bright (77.3 cd/m^2) or dark (22.4 cd/m^2).

279

280   Across trials, the probe flash could either appear 7 deg above the saccade target

281   location (i.e. above the intended saccade landing position) or 7 deg below the

282   saccade target location, and the subjects' task was to indicate, by pressing one of

283   two buttons on a response box, whether the flash appeared above or below screen

284   center in every trial. If the subjects did not see the flash, they had to guess its

285   location. Note that with our display geometry, the retinotopic position at which the

286   probe flash could appear was visually-stimulated before the saccade by the display

287   itself (i.e. a uniform luminance) rather than the (very) dark surround of the laboratory.

288   Thus, across the saccade, the possible retinotopic location of the flash was swept

289   across a uniform luminance rather than across the outer edge of the display.

290

291   We collected psychometric curves of flash perception as follows. Across trials, and

292   for a given condition (for example: the combination of dark background; negative

293   contrast flash; flash time 24 ms after saccade detection), we used an adaptive

294   approach to select flash luminance levels resulting in threshold performance (Idrees,

295   Baumann, Franke, et al., 2020). Briefly, in the first of the two sessions for this

296   condition (and similarly for all other conditions), we used a QUEST procedure

297   (Watson & Pelli, 1983) for each flash polarity, each background luminance, and each

298   post-saccadic flash time aiming to achieve a percent correct of 75% over 60 trials.

299   Then, after the threshold contrast was found for each QUEST procedure, in the

300   second session, we introduced, for each condition, 6 additional contrast levels

301   around the detected perceptual threshold with the adaptive procedure, in order to

302   obtain more samples for the psychometric curve of each subject. This is similar to

303   what we did in our recent work (Idrees, Baumann, Franke, et al., 2020).

304

305   Note that in this and all other conditions and analyses throughout this study, we refer

306   to "threshold" as the absolute value of the probe contrast that was used (whether the

307   probe was a luminance increment or decrement relative to the background).

308   However, we always also explicitly specify whether the probe was of positive

309   (luminance increment) or negative (luminance decrement) polarity. This way, it is

310   simpler to quantitatively compare saccade-related threshold elevations for both types

311   of probe flashes.

312

313   We collected 1920 trials per subject in this condition.

314

315   *(2) Real saccades across a vertical visual stripe:* This condition was identical to

316   condition 1 except that each saccade crossed a vertical luminance stripe of width 2.4

317   deg. The stripe was centered horizontally on the midway point between initial and

318   final fixation spot locations, and it spanned the full vertical extent of the display (Fig.

319   1A, middle). Therefore, on every trial, the display was configured to have two vertical

320   luminance stripes at 5.7 deg either to the right or left of display center. The left stripe

321   was crossed by rightward saccades starting from the left side of the display, and the

322   right stripe was crossed by leftward saccades. The rest of the display was the same

323   as in condition 1. Across trials, we varied the luminance of either the background or

324   the stripes. Specifically, the stripes had the dark luminance when the rest of the

325   display had the bright luminance, and vice versa (same luminance values as in

326   condition 1). This way, the eye could start and land on either a dark or bright

327   luminance region (like in condition 1), but the difference is that the gaze would have

328   had to cross a luminance stripe of the other luminosity during the saccade. Like in

329   condition 1, note that with our display geometry, the retinal positions of the probe

330   flash locations were visually-stimulated by the display before the saccade (rather

331   than by the much darker surround in the laboratory environment around the display).

332

333   We collected 1920 trials per subject from this condition.

334

335   *(3) Real saccades across a vertical luminance edge:* In this condition, the display

336   was split (along the horizontal dimension) into three areas (one central and two

337   flanks; Fig. 1A, bottom): the central region had either a bright or dark luminance, and

338   the flanks were the opposite. The vertical edge between the central region and either

339   of the two flanking regions was at 5.7 deg horizontally from display center, which is

340   halfway between the initial and final fixation spot's horizontal locations. As a result,

341   there was a vertical edge across which the same saccades as in conditions 1 and 2

342   were made. The bright and dark luminances on either side of the vertical edge were

343   the same as those of the bright and dark background luminances in conditions 1 and

344   2, and they were varied across trials (some trials had the central area being bright,

345   and others had the flanking areas being bright, independently of whether the saccade

346   was rightward or leftward). Thus, in this condition, the saccade landed on either a

347   bright or a dark luminance level (like in conditions 1 and 2); however, critically, the

348   initial luminance level at saccade onset was always different from the final luminance

349   level (Fig. 1A, bottom). Moreover, the probe flashes (whether luminance increments

350   or luminance decrements) were always presented relative to the luminance level at

351   the end of the saccade. That is, the probe flashes appeared on either bright or dark

352   backgrounds (like in conditions 1 and 2).

353

354   We collected 1920 trials per subject from this condition.

355

356   *(4) Simulated saccades across a vertical luminance edge:* In this condition, the

357   subjects maintained fixation at display center, and a visual transient like that in

358   condition 3 was introduced. That is, the display had a central region that was either

359   bright or dark and two flanking regions around it with the opposite brightness from the

360   central region (Fig. 2A). Thus, there was a vertical edge, which was then translated

361   horizontally to simulate a saccade across this edge. To achieve translation of the

362   vertical edge across the fovea, we translated the whole displayed texture (i.e. both

363   the central and flanking regions) horizontally at high speed (see the next paragraph

364   for details on handling monitor edge effects). The resulting "simulated" saccade had

365   parameters similar to those used in our recent work (Idrees, Baumann, Franke, et al.,

366   2020). Briefly, we translated the texture (and, therefore, the vertical edge) by 1.9 deg

367   every display frame (of approximately 12 ms) for 6 display frames, corresponding to

368   an overall translation of 11.4 deg in 72 ms. This resulted in a high-speed translation

369   of the vertical edge across the fovea during maintained fixation. The translation

370   matched, in amplitude and duration, the amplitudes and durations of the real

371   saccades that the subjects made in conditions 1-3 above. Specifically, in these

372   conditions, the average saccade amplitude and duration were 11.37 +/- 0.14 deg and

373   74.89 +/- 2.05 ms, respectively, across all trials from all subjects (mean value +/-

374   s.e.m.).

375

376   The sequence of events in a given trial was as follows. An initial fixation spot

377   appeared at trial onset at the center of the display. The two vertical edges were at 5.7

378   deg to the left and right of the fixation spot location (Fig. 2A). After a random time of

379   800-1700 ms, the high-speed translation was started. For a leftward translation, the

380   right vertical edge shifted to become now located at the initial location of the left

381   vertical edge after the entire sequence had ended, and vice versa for a rightward

382   texture shift. To handle display monitor edge effects, we treated the initial displayed

383   pattern (i.e. the whole of the combination of central region and two flanks) as a

384   horizontally periodic pattern. As a result, when a leftward shift happened, the

385   rightward flank translated to become the central region, and a new rightward flank

386   that was the same luminance as the original central region appeared. The

387   corresponding scenario played out for a rightward shift. A probe flash appeared

388   similar to the other conditions described above.

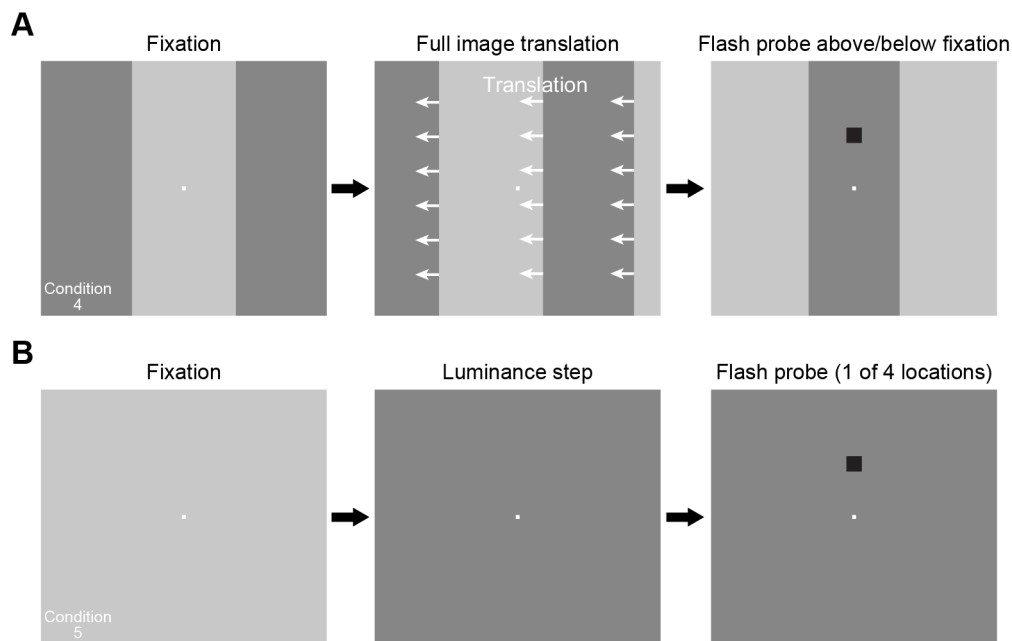389

390

391

392   **Figure 2 The visual-only conditions tested in our study. (A)** In condition 4, subjects fixated the center
393   of the display, and the background was identical to that of condition 3 in Fig. 1. After initial fixation was
394   established, the whole background translated horizontally to shift one of the two vertical edges across
395   gaze position. After the translation, gaze was now aimed at a different background luminance. This
396   condition mimicked the real saccade version in condition 3. Note that during translation, we treated the
397   texture as being horizontally periodic (in the shown example, this meant that a bright background was
398   revealed on the right edge of the display monitor during leftward translation). At different times relative
399   to translation onset, we presented a flash either above or below fixation, similar to Fig. 1A. In this case,
400   the flashes could be presented either before or after translation onset (Methods). When presented after
401   translation onset, the timing was such that they were presented over the new background luminance
402   after translation end (that is, the edge had crossed display center even for the earliest flash time after
403   translation onset). **(B)** In condition 5, the subjects fixated the center of a uniform display, and we
404   changed the luminance of the background (from dark to bright or vice versa). Relative to this transient,
405   a probe flash could happen at similar times to those used in **A**. Note that in this condition only, we had
406   four possible probe flash locations, because this experiment was a replication of our earlier version of it
407   in (Idrees, Baumann, Franke, et al., 2020; Idrees, Baumann, Korympidou, et al., 2020).

408

409

410

411   Across trials, we picked 2 times of probe flashes after the onset of the simulated

412   saccades (47 and 59 ms) and also 2 times of probe flashes before the onset of the

413   simulated saccades (24 and 35 ms before simulated saccade onset). The use of

414   probe flashes before simulated saccade onset allowed us to demonstrate existence

415   of pre-transient suppression, which provides a logical link to our other work (Idrees,

416   Baumann, Franke, et al., 2020), and which also demonstrates that our lack of pre-

417   saccadic flash times in conditions 1 to 3 above does not necessarily mean that there

418   was no pre-saccadic suppression in these conditions. All other parameters of the

419   experiment were similar to conditions 1 to 3.

420

421   We collected 1920 trials per subject from this condition.

422

423   *(5) Fixation with a luminance change:* In this final condition, subjects maintained

424   fixation at the center of a uniform display, and the visual transient now consisted of a

425   change in background luminance from dark to bright, or vice versa (Fig. 2B). Probe

426   flashes could appear either before (24 or 35 m) or after (35, 71, or 106 ms) the

427   luminance change, like in condition 4. Note that in this condition only, we used a four-

428   alternative forced choice paradigm as opposed to the two-alternative forced choice

429   paradigm in all other conditions. So, instead of just presenting a probe flash 7 deg

430   above or below the fixation (or saccade) target location, the probe flash could now

431   appear at 7 deg in any of the four cardinal directions around the fixation spot (right,

432   left, up, or down; Fig. 2B). Subjects had to press one of four buttons corresponding to

433   the four possible flash locations. The reason that we used four alternatives in this

434   case is that fixation was always at the center of the display and that the display itself

435   was uniform (allowing us to probe horizontal flash locations without worrying about

436   "pre-saccadic" retinal image regions of horizontal flash locations being visually

437   stimulated by the dark laboratory surround instead of the actual display, or by

438   another luminance on the display like in condition 4). Another reason for using four

439   alternatives is that this condition involved collecting new data from a similar condition

440   (with four alternatives) that we had recently run (Idrees, Baumann, Franke, et al.,

441   2020; Idrees, Baumann, Korympidou, et al., 2020). All other parameters and

442   procedures were the same as in all other conditions.

443

444   We collected 2400 trials per subject from this condition.

445

446

447 *Data analysis*

448 We detected saccades and microsaccades using our laboratory's established

449 methods (M. E. Bellet, Bellet, Nienborg, Hafed, & Berens, 2019; Chen & Hafed,

450 2013; Hafed, 2013). For all trials with fixation (conditions 4 and 5), we ensured that

451 there were no microsaccades from -200 to +50 ms relative to probe flash onset. This

452 allowed us to avoid potential changes in visual sensitivity around the time of

453 microsaccades (Chen & Hafed, 2017; Chen et al., 2015; Hafed, Chen, & Tian, 2015).

454 Trials that contained microsaccades in the above intervals were excluded from

455 subsequent analyses. Similarly, for trials with real saccades, we excluded trials with

456 saccades before instruction (i.e. before fixation spot jump) and also trials with

457 saccadic reaction times >500 ms from saccade target onset, and we confirmed that

458 the flash times relative to saccade onset (after post-hoc offline saccade detection)

459 indeed clustered into 4 different time points, as designed in the task (see above and

460 Fig. 1B-D).

461

462 We analyzed the proportion of correct trials as a function of probe flash Weber

463 contrast (i.e. absolute value of luminance difference of flash from background

464 luminance, divided by the background luminance). We did this for each flash

465 luminance used, and independently for whether the probe flash consisted of a

466 luminance increment or a luminance decrement relative to background luminance.

467 We also did this for each flash time used (for real saccades, we classified all flash

468 times into 4 "clusters" of flash times centered around the mean values measured

469 after offline saccade detection; see Fig. 1B-D). Across contrasts (for either

470 increments or decrements), we obtained a psychometric curve fit of perceptual

471 performance using the psignifit 4 toolbox (Schutt, Harmeling, Macke, & Wichmann,

472 2016). Briefly, we used, via the toolbox, a beta-binomial model for the psychometric

473 curve. We defined the perceptual threshold as the absolute Weber contrast value

474 resulting in a correct performance level that was at either 75% of the total dynamic

475 range of the fitted psychometric curve (for conditions 1-4 with two-alternative forced

476 choices) or 62.5% of the total dynamic range of the psychometric curve (for condition

477 5 with four-alternative forced choices). If there was perceptual suppression of

478 sensitivity, then the threshold contrast was elevated. Thus, plots of threshold contrast

479 indicate maximal suppression when the perceptual thresholds are high.

480

481   For each background luminance over which a given flash appeared (dark or bright),

482   and for each flash time, we calculated a psychometric curve for either flashes

483   consisting of luminance increments or luminance decrements (i.e. flash stimulus

484   polarity). We used the longer flash times after visual transient onset (either caused by

485   real saccades or visual display updates during fixation) to confirm that there was

486   perceptual recovery with time (as expected). Therefore, elevations of threshold

487   contrast above the threshold values at such longer post-transient times were

488   evidence for perceptual suppression.

489

490   To summarize results across subjects, we first estimated perceptual thresholds for

491   each subject, and we then averaged the thresholds across subjects, with indications

492   of inter-subject variance in all figures. To perform statistics, we used two-way

493   ANOVA's testing the influences of flash time and condition on perceptual thresholds.

494   We also sometimes performed individual t-tests comparing pairs of conditions at one

495   given flash time; typically, this was the shortest flash time after saccade onset (or

496   after texture translation or contrast change in conditions 4 and 5) since this time was

497   the time associated with maximal perceptual suppression. This flash time was

498   therefore of most interest when comparing suppression strength across the different

499   conditions. It should also be noted that in conditions 4 and 5, when we had "pre-

500   transient" flashes, the flash appeared on a background that was different from the

501   background for flash onsets occurring after the visual transient. Therefore, in all

502   figures, we always pooled data points based on the background luminance on which

503   a flash actually appeared. For example, pre-transient flashes in condition 4 with, say,

504   a translation from bright to dark background were plotted as flashes over a bright

505   background, whereas post-transient flashes were plotted as flashes over a dark

506   background. This way, we always compared perception with a similar relationship

507   between flash luminance and background luminance at the time of the flash. In

508   statistical analyses of condition 5, we also pooled, within each subject, the longest

509   two flash times after background luminance change together. This was because

510   these two times showed the same effects anyway.

511

512 **Results**

513

514 We assessed the visual contributions to perceptual saccadic suppression by

515 measuring perceptual sensitivity for brief flashes presented around the time of

516 saccades across a variety of image types. We found that perceptual saccadic

517 suppression has a large component of visual dependencies built into it. Critically, we

518 also compared such sensitivity to situations in which there were no saccades, but in

519 which conceptually comparable visual transients like those associated with saccades

520 were experimentally introduced. With such simulated saccades, we found similar

521 suppression as during real saccades, despite the absence of saccadic motor

522 commands, and the same dependencies on visual context. In all cases, we

523 compared perceptual sensitivity to a baseline case in which saccades were made

524 across a uniform background. These results confirm and extend our recent

525 observations that were motivated by recordings of ex-vivo retinal ganglion cell activity

526 in multiple species (Idrees, Baumann, Franke, et al., 2020; Idrees, Baumann,

527 Korympidou, et al., 2020), and they are in line with other psychophysical evidence in

528 the literature. This allows us to conclude that perceptual saccadic suppression may

529 fundamentally be a visual phenomenon. In what follows, we describe how we

530 reached this conclusion.

531

532

533 *Saccades across a local luminance feature are associated with much stronger*

534 *perceptual suppression than saccades across a uniform background*

535 We collected perceptual threshold measurements across saccades. In one condition

536 (condition 1), subjects made predominantly horizontal oblique saccades across a

537 uniform background. In another condition, the saccades were made across a 2.4 deg

538 wide luminance stripe relative to background luminance, but the luminances at both

539 saccade start and saccade end were the same (condition 2). That is, the display

540 consisted of a uniform background with a vertical stripe (of 2.4 deg width) midway

541 between the start and end points of the saccade (see Fig. 1). We detected saccade

542 onset online, and we presented probe flashes at 4 different times after saccade

543 detection (Methods). The presented peri-saccadic probe flashes occurred on top of

544 the same background luminance in both the baseline control condition (saccades

545 across a uniform background) as well as the luminance feature condition (saccades

546 across a luminance stripe on an otherwise uniform background). Subjects had to

547 decide, on every trial, whether the probe flash appeared above or below the line of

548 site (Methods), and we varied flash contrasts in order to collect full psychometric

549 curves.

550

551 Figure 3 shows example psychometric curves of perceptual detectability obtained

552 from an example subject in the two conditions and at flash times of approximately 40

553 ms (Fig. 3A) and 63 ms (Fig. 3B) after saccade onset. In this figure, we show results

554 only from the dark background condition (Methods), and also when the luminance of

555 the probe flash was a decrement relative to background luminance (i.e. negative

556 stimulus polarity). Note that in this and all other figures, we depict the absolute value

557 of Weber contrast, to aid comparison of effects between positive-contrast and

558 negative-contrast probe flashes. Flashes immediately after saccade detection (Fig.

559 3A) were associated with elevated perceptual thresholds in both conditions: this is

560 evidenced by rightward shifts of the psychometric curves for the early time compared

561 to the late one (compare the correspondingly colored curves in Fig. 3A and Fig. 3B).

562 However, the effect was much stronger for condition 2, in which saccades crossed

563 over a bright luminance stripe of 2.4 deg width. Specifically, at 40 ms (Fig. 3A), the

564 absolute value of perceptual threshold was at >0.8 Weber contrast in condition 2 and

565 at only <0.15 Weber contrast in condition 1. Similarly, at the later time point, even

566 after partial perceptual recovery (Fig. 3B), the absolute value of threshold in condition

567 2 was still at a level of almost 0.3 Weber contrast, but it was already at a level <0.09

568 in condition 1. Thus, perceptual saccadic suppression is much stronger when

569 saccades are made across a luminance stripe than across a uniform background.
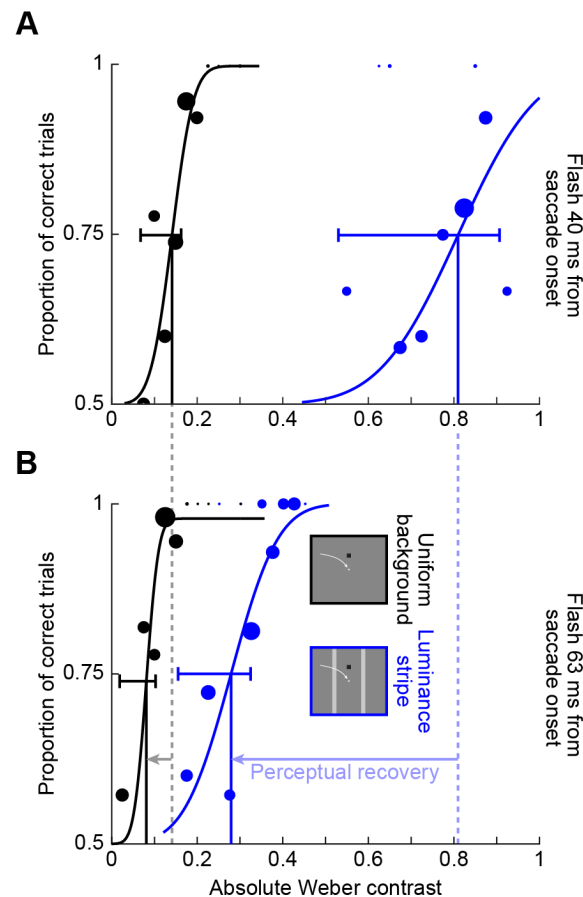
570

571

572

573

Figure 3 Much stronger saccadic suppression across a luminance stripe than across a uniform background. Example psychometric curves of perceptual detectability from one sample subject, for dark probe flashes over a dark background. Circles show individual data points, with the size of the circle scaled based on the numbers of observations collected. The blue curves show psychometric curves when the saccade crossed a luminance stripe (condition 2), whereas the black curves show the results obtained when the saccade was made across a uniform background (condition 1); see the schematic legend in **B**. Vertical lines indicate the perceptual threshold values in each condition, and horizontal error bars show 95% confidence intervals for each psychometric curve (obtained using the psignifit 4 toolbox; Methods). **(A)** Data for probe flashes presented immediately after online saccade detection (40 ms after actual saccade onset; first time cluster in Fig. 1B-D). There was a much larger rightward shift in the psychometric curve in the case of condition 2 when compared to condition 1. **(B)** Data for a later flash time (63 ms after saccade onset; third time cluster in Fig. 1B-D). Both curves recovered at this time point (i.e. shifted leftward relative to **A**; horizontal leftward arrows), but the blue curve still showed much more suppression (i.e. rightward shift) compared to the black curve.

592 Across subjects, we made very similar observations. For example, the blue curve in

593 Fig. 4A shows the average psychometric curve obtained across all subjects (the

594 average of all subjects' individual psychometric curves) in condition 2 for the first

595 flash time (40 ms after saccade onset). This curve was shifted much more strongly to

596 the right than the black curve in the same panel. The black curve summarizes the

597 results across subjects with only a uniform background (condition 1). Similarly, Fig.

20

598   4B shows recovery results at the 63 ms time point in the same format, again

599   consistent with Fig. 3. To summarize the effect size and time course to recovery

600   across the two conditions, we then estimated the perceptual threshold for a given

601   condition as the absolute value of Weber contrast in each psychometric curve

602   resulting in a correct performance level of 75% of the dynamic range (Methods,

603   compare the vertical lines in Fig. 3) (Idrees, Baumann, Franke, et al., 2020). Figure

604   4C plots the absolute threshold contrasts at all probe flash times: in blue for condition

605   2 and in black for condition 1. Error bars denote s.e.m. across subjects (Methods). As

606   can be seen, there was much stronger suppression (larger increase in the perceptual

607   threshold contrast) for saccades across the luminance stripe (blue) when compared

608   to saccades across the uniform background (black), and this also persisted as a

609   function of time. Statistically, a two-way ANOVA revealed a highly significant effect of

610   both factors of flash time ($F_{(3,40)} = 43.3$, $p < 10^{-11}$) and condition ($F_{(1,40)} = 151.1$, p

611    $< 10^{-14}$). Moreover, there was also a significant interaction between the two factors

612   ($F_{(3,40)} = 29.2$, $p < 10^{-9}$). Post hoc, we compared the thresholds of condition 1

613   (mean +/- s.e.m.: 0.13 +/- 0.02 Weber contrast) and condition 2 (0.95 +/- 0.1 Weber

614   contrast) at 40 ms (the time of maximal suppression in our experiments). There was

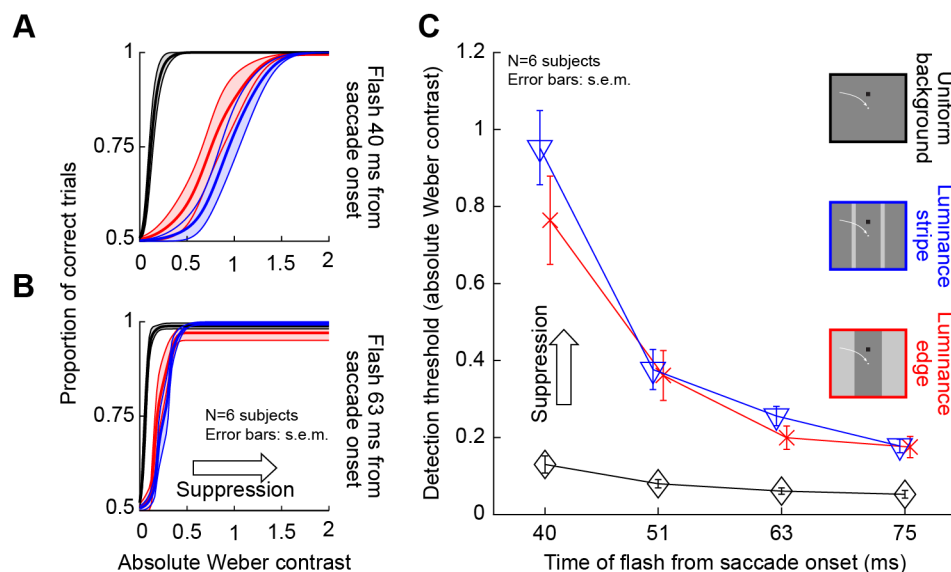615   a highly significant difference around the time of maximal suppression ($t(5) = 7.9$, p <

616   0.001).

617

618

619

620   **Figure 4 Systematically stronger saccadic suppression across a luminance stripe or luminance**
621   **edge than across a uniform background. (A)** Average psychometric curves of perceptual detectability
622   from all subjects when the probe flashes occurred 40 ms after saccade onset (first time cluster in Fig.
623   1B-D). Black: psychometric curve for condition 1, when saccades were made across a uniform
624   background. Blue: psychometric curve when saccades crossed a luminance stripe (condition 2). Red:

21

625 psychometric curve for condition 3, when saccades crossed a luminance edge. In all cases, error bands
626 denote s.e.m. across subjects. Perceptual thresholds were elevated much more for conditions 2 and 3
627 than for condition 1. **(B)** Same as in **A** but for a later time point (63 ms). There was perceptual recovery,
628 but saccadic suppression was still stronger in conditions 2 and 3 than in condition 1; the subjects always
629 had higher thresholds than in condition 1 (also see **C**). **(C)** Perceptual thresholds (average across
630 subjects) for each flash time after saccade onset. Higher values mean stronger saccadic suppression.
631 Error bars denote s.e.m. across subjects. Note that the time values on the x-axis are the average flash
632 times obtained after offline saccade detection (Methods and Fig. 1B-D). Also note that for each average
633 flash time, we slightly jittered the x-axis position of each data point to not mask individual data points
634 and their error bars (also true in subsequent figures below). There was much stronger saccadic
635 suppression in conditions 2 and 3 than in condition 1.

636

637

638

639 *Different pre- and post-saccadic visual stimulation is also associated with strong*

640 *perceptual saccadic suppression*

641 We next asked whether the final luminance on which the probe flashes appeared

642 peri-saccadically needed to be the same as the "pre-saccadic" luminance at the line

643 of sight for us to obtain the above results. To test this, we replaced the stripe used in

644 condition 2 with a luminance edge (condition 3; Methods; red curves in Fig. 4). That

645 is, this time, the subjects initially fixated a bright background, and they then made

646 saccades across a vertical edge, such that the probe flashes (and saccade landing

647 positions) were now over a dark background. We then compared perceptual

648 suppression to that obtained with saccades across a uniform dark background

649 (condition 1). The same strong difference in saccadic suppression relative to the

650 uniform dark background was observed (Fig. 4, now compare red to black curves).

651 For example, at the first flash time after saccade onset (Fig. 4A, C), the average

652 perceptual threshold in both conditions 2 and 3 was >0.75 Weber contrast, whereas it

653 was only 0.13 Weber contrast when saccades were made across a uniform

654 background (Fig. 4C). Moreover, statistically, there was still a highly significant effect

655 of time ($F(3,40) = 19$, $p < 10^{-7}$) and condition ($F(1,40) = 70$, $p < 10^{-9}$), when now

656 comparing condition 3 to condition 1 (two-way ANOVA) instead of comparing

657 condition 2 to condition 1 as we had done above. There was also a significant

658 interaction effect ($F(3,40) = 11.4$, $p < 10^{-5}$). Moreover, a paired post hoc t-test

659 highlighted a difference at at 40 ms ($t(5) = 6.72$, $p = 0.001$); condition 1: 0.13 +/- 0.02

660 s.e.m. Weber contrast, and condition 3: 0.76 +/- 0.11 s.e.m. Weber contrast. In fact,

661 when we compared threshold contrasts across subjects in both conditions 2 and 3

662 together (colored curves in Fig. 4C), we found that suppression was equally strong

663 for both of these conditions. A two-way ANOVA with the factors time and condition (2

22

664   versus 3) revealed no significant interaction between the factors ($F_{(3,40)} = 0.9$, $p =$
665   0.45) and no significant effect of the condition ($F_{(1,40)} = 2.2$, $p = 0.15$). However,
666   expectedly, the effect of flash time was highly significant ($F_{(3,40)} = 48.5$, $p < 10^{-12}$).
667

668   Therefore, saccadic suppression is also enhanced when gaze crosses a luminance
669   edge rather than a luminance stripe, replicating results from an earlier study (Maij,
670   Matziridi, Smeets, & Brenner, 2012). The difference here is that in our current
671   experiments, we assessed thresholds explicitly, by collecting full psychometric
672   curves, allowing a more sensitive measure of perceptual sensitivity. We also varied
673   stimulus polarities of the flashes, and even replaced saccades with image
674   translations, as we describe in more detail shortly.
675

676   It is important to note that saccadic suppression still occurred over a uniform
677   background (condition 1), albeit in a weak fashion. To confirm this, we statistically
678   assessed perceptual detectability in condition 1 with a dark background, and we
679   found that there was elevation of contrast immediately after saccade detection when
680   compared to the latest two flash times after saccade onset in Fig. 4C (black): a one-
681   way ANOVA with flash time as factor was significant ($F_{(3,20)} = 6.2$, $p = 0.004$), and a
682   post hoc test revealed significant differences for the perceptual thresholds at 40 and
683   63 ms ($p = 0.01$) and 40 and 75 ms ($p = 0.004$). Similar results also occurred for a
684   bright background (we address the influence of background luminance more explicitly
685   shortly). This extends the results of (Maij et al., 2012) in an important way.
686   Specifically, in that study, it could appear that there was no saccadic suppression at
687   all with a uniform background. However, we think that measuring contrast thresholds
688   in our experiments was a more sensitive measure of perceptual sensitivity. The
689   approach of Maij et al could result in floor or ceiling effects, potentially masking a mild
690   amount of suppression (which we observed).
691

692

693   *A visual dependence of saccadic suppression also emerges when considering the*
694   *luminance of the background across which saccades are made*
695   The above results indicate that the visual conditions across which saccades are
696   made do matter for perceptual saccadic suppression, as we also recently argued
697   (Idrees, Baumann, Franke, et al., 2020). To further demonstrate that perceptual

698   saccadic suppression does indeed have a strong visual component, we next checked

699   whether the luminance of the background mattered for the strength of suppression. In

700   our experiments, saccades could be made in condition 1 across either a bright or a

701   dark background (Methods). Similarly, in conditions 2 and 3, the final landing position

702   of the saccades, and therefore the final possible probe flash locations, could be

703   either on a bright background or a dark background. In the description of results so

704   far we have focused only on the dark background condition. We now describe the

705   threshold contrasts that were obtained when the probe flashes appeared on a bright

706   background instead.

707

708   Fig. 5A, B show average psychometric curves across subjects for the first flash time

709   after saccade detection (approximately 40 ms from saccade onset). Here, we directly

710   compare trials having a dark background at flash occurrence (solid lines, replicated

711   from Fig. 4A) with trials having a bright background at flash occurrence (dashed

712   lines). In Fig. 5A, the data for condition 2 are shown, and in Fig. 5B, the data for

713   condition 3 are shown. In both cases, saccadic suppression was much stronger over

714   a dark landing position than over a bright landing position. This effect can be better

715   seen through plots of the time course of saccadic suppression in the two conditions

716   (Fig. 5C). Statistically comparing bright versus dark backgrounds, as well as time, in

717   two-way ANOVA's confirmed that there was a strong effect of background luminance

718   (and time) on saccadic suppression. For both conditions, a two-way ANOVA revealed

719   significant interactions (condition 2: $F(3,40) = 20.9$, $p < 10^{-7}$; condition 3: $F(3,40) =$

720   7.1, $p < 0.001$) between the factors, as well as highly significant main effects for time

721   (condition 2: $F(3,40) = 52.9$, $p < 10^{-13}$; condition 3: $F(3,40) = 24.4$, $p < 10^{-8}$) and

722   background luminance (condition 2: $F(1,40) = 102.2$, $p < 10^{-11}$; condition 3: $F(1,40) =$

723   24.2, $p < 10^{-4}$). Note that for simplicity, we still only considered flashes consisting of

724   luminance decrements relative to the background (i.e. of negative stimulus polarity),

725   exactly like in all analyses above. We will explicitly describe the impact of flash

726   luminance polarity relative to the background in a subsequent analysis. In any case,

727   threshold elevations were much stronger with dark backgrounds than with bright

728   backgrounds.

729

730   Incidentally, for saccades across a uniform background (condition 1), we did not

731   observe a significant influence of background luminance on the strength of saccadic

732   suppression. A two-way ANOVA with the factors time and background luminance

733   showed no interaction between the factors ($F_{(3,40)} = 0.05$, $p = 0.98$). As expected,

734   since suppression still took place in this condition, the main effect of time was still

735   significant ($F_{(3,40)} = 13.5$, $p < 10^{-5}$). However, the factor of background luminance

736   was not significant ($F_{(1,40)} = 0.9$, $p = 0.34$). This could reflect the small effect size in

737   this condition in general.
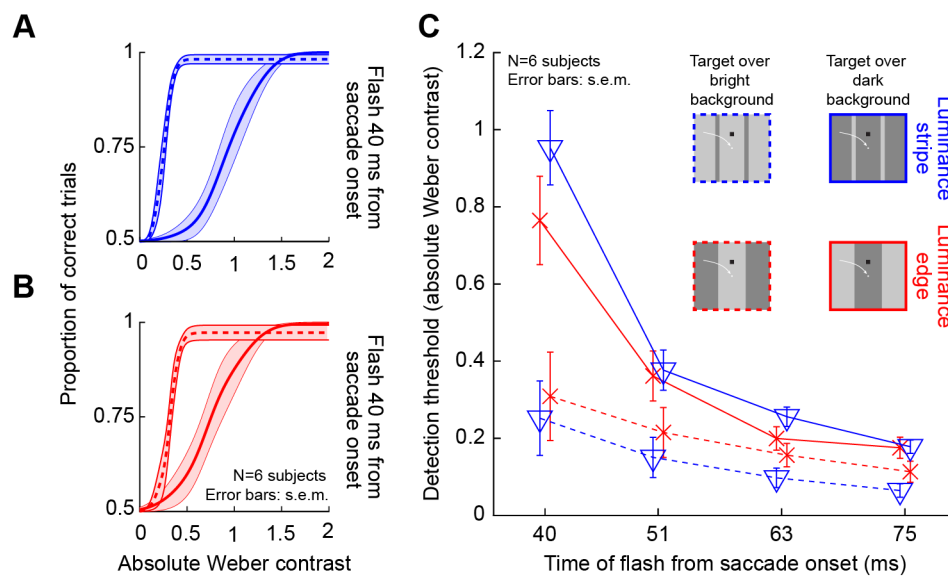
738

739

740

741

Figure 5 Stronger saccadic suppression over dark backgrounds, whether with luminance edges or luminance stripes. (A) Average psychometric curves of perceptual detectability from all subjects in condition 2, and for probes occurring 40 ms after saccade onset (i.e. the first time cluster in Fig. 1B-D). Solid indicates flashes over a dark background (i.e. saccades starting and ending on a dark patch, but crossing a bright stripe), and dashed indicates flashes over a bright background (i.e. saccades starting and ending on a bright patch, but crossing a dark stripe). In both cases, the probe flashes had negative luminance polarity (i.e. they were luminance decrements relative to the background). Saccadic suppression was stronger with dark backgrounds than with bright backgrounds. Error bands denote s.e.m. across subjects. **(B)** Similar results were obtained in condition 3. Flashes over a dark background (when saccades were made from a bright to a dark patch) were associated with stronger suppression than flashes over a bright background (when saccades were made from a dark to a bright patch). **(C)** Perceptual thresholds (averaged across subjects) for each flash time after saccade onset. Higher values mean stronger saccadic suppression, and error bars denote s.e.m. across the subjects. In both conditions 2 and 3, flashes over a dark background (solid) were associated with much stronger saccadic suppression than flashes over a bright background (dashed). All other conventions are similar to Fig. 4.

757

758

759

760   Therefore, the results of Fig. 5 further illustrate the strong visual dependencies of

761   perceptual saccadic suppression. When (negative polarity) probe flashes were

762   presented over dark backgrounds, perceptual thresholds were elevated much more

763   around the time of saccades than when the same negative polarity flashes (of the

764   same contrast) were presented over bright backgrounds. Earlier work related to

765   condition 3 did not analyze the effects of background luminance (Maij et al., 2012),

766   and our recent experiments only used textured backgrounds (Idrees, Baumann,

767   Franke, et al., 2020). Interestingly, the present results clarify why saccadic

768   suppression was so strong in these recent experiments (Idrees, Baumann, Franke, et

769   al., 2020). This was because a visual feature seems to be necessary for boosting the

770   saccadic suppression effect.

771

772

773   *Flash luminance polarity interacts with background luminance to modulate the*

774   *strength of saccadic suppression*

775   We observed above that saccades across luminance-defined features are associated

776   with strong perceptual suppression (Figs. 3, 4), and that background luminance

777   interacts with the presented brief flashes to modulate the strength of suppression

778   (Fig. 5). However, in all of our analyses so far, we only considered negative polarity

779   probe flashes (that is, flashes consisting of luminance decrements relative to the

780   surrounding background luminance). To check whether probe flash polarity

781   constitutes an additional visual dependence of perceptual saccadic suppression, we

782   then turned our attention to analyzing trials with positive polarity probe flashes (that

783   is, flashes that had luminance increments relative to the surrounding background

784   luminance).

785

786   In Fig. 6, we plotted the threshold contrasts across subjects for positive and negative

787   polarity flashes in conditions 1, 2, and 3. In Fig. 6A, C, we show the results with

788   flashes presented over a dark background, and in Fig. 6B, D, we show the results

789   with flashes presented over a bright background. The top row of the figure (Fig. 6A,

790   B) shows results from condition 2 (blue), whereas the bottom row (Fig. 6C, D) shows

791   results from condition 3 (red). For each condition, the different shades of color denote

792   whether the flash had negative polarity (saturated colors; these are data replicated

793   from the previous figures) or positive polarity (unsaturated colors) relative to the

794   background. Note that both rows also show the results from condition 1 with a

795   uniform background for reference (black and gray curves). Also note that the y-axes

796   in Fig. 6A, C are different from those in Fig. 6B, D because of the differential impact

797   of background luminance that we described in Fig. 5. As can be seen from Fig. 6A,

798   C, negative polarity probe flashes over dark backgrounds had stronger saccadic

799   suppression (higher detection thresholds) than positive polarity probe flashes over

800   the same background, especially at the time of peak saccadic suppression (40 ms).

801   For example, immediately after saccade onset in conditions 2 and 3, perceptual

802   thresholds were at 0.95 and 0.76 Weber contrast across subjects for negative

803   polarity flashes, respectively (Fig. 6A, C, colored curves). For positive polarity

804   flashes, the thresholds were elevated to only 0.69 and 0.54, respectively.

805   Statistically, this difference between positive and negative polarity flashes was

806   significant at 40 ms in both condition 2 ($t(5) = 6.69$, $p = 0.001$; positive polarity mean

807   and s.e.m.: 0.95 +/- 0.1 Weber contrast; negative polarity: 0.69 +/- 0.07 Weber

808   contrast) and condition 3 (paired t-test: $t(5) = 3.31$, $p = 0.02$; positive polarity mean

809   and s.e.m.: 0.76 +/- 0.11 Weber contrast; negative polarity: 0.54 +/- 0.07 Weber

810   contrast). Interestingly, over a bright background (Fig. 6B, D), both conditions 2 and 3

811   did not show any difference in the strength of saccadic suppression between positive

812   and negative polarity flashes (Fig. 6B, D, colored curves). Therefore, there was an

813   interaction between flash polarity and background luminance in modulating the

814   strength of perceptual saccadic suppression.

815

816   It is also interesting that for condition 1, similar effects still existed for flash luminance

817   polarity (Fig. 6, black and gray curves) despite the very weak perceptual saccadic

818   suppression that occurred: it was still the case that negative polarity flashes over a

819   dark background (mean threshold 0.13 +/- 0.02 s.e.m. Weber contrast) tended to

820   cause stronger saccadic suppression than positive polarity flashes (mean threshold:

821   0.09 +/- 0.01 s.e.m.) over the same background ($t(5) = 3.6$, $p = 0.016$ Weber

822   contrast). Thus, our analyses of probe flash stimulus polarity in all saccade

823   conditions (1, 2, and 3) provide further evidence that perceptual saccadic

824   suppression has strong visual dependencies.
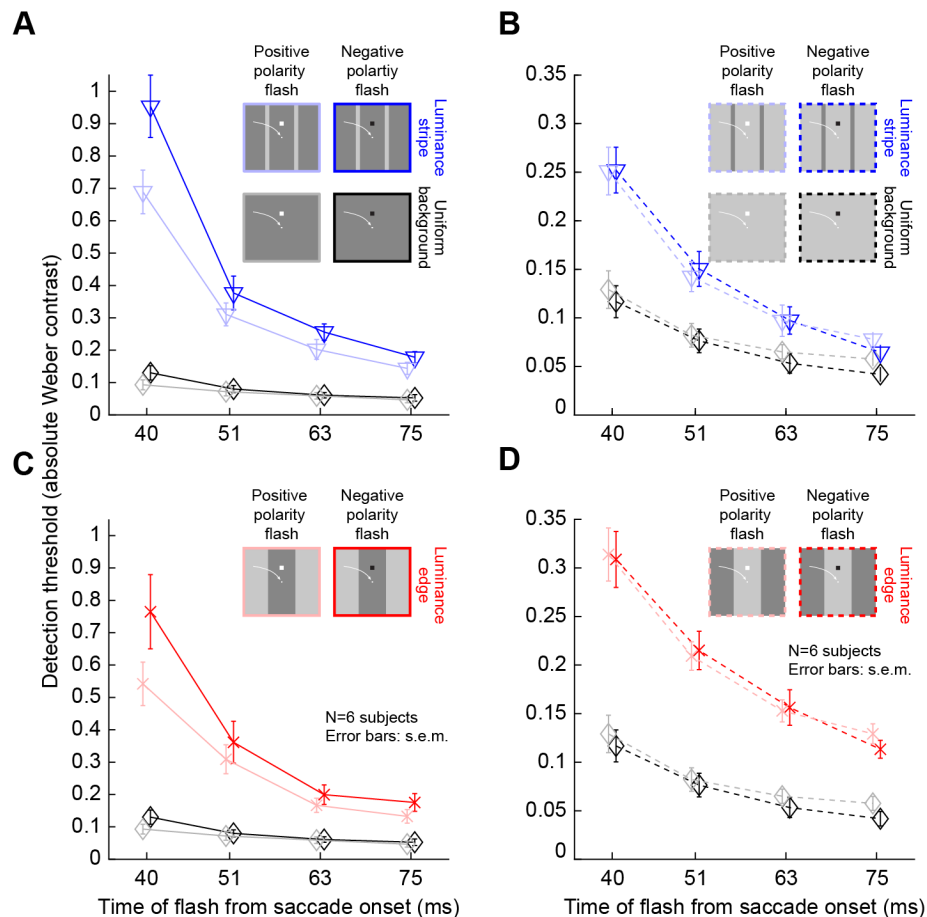
825

826

827

Figure 6 Stronger saccadic suppression for negative polarity flashes over dark backgrounds when compared to positive polarity flashes. Perceptual thresholds across subjects as a function of flash time after saccade onset (error bars denote s.e.m. across subjects). **(A)** Data from condition 2 (blue) and condition 1 (black) with flashes appearing over a dark background. The saturated colors show results with negative polarity flashes, and the unsaturated colors show results with positive polarity flashes. Consistent with earlier figures, perceptual saccadic suppression was much stronger (higher absolute values of perceptual thresholds) in condition 2 than in condition 1 (compare colored to black curves). Within each condition, saccadic suppression was stronger with negative polarity flashes than positive polarity flashes, especially near the time of peak saccadic suppression (40 ms). **(B)** With bright backgrounds, the effects of flash polarity were absent (but suppression was still stronger than in condition 1). Note that the y-axis is different from **A**, because suppression was weaker for flashes over bright backgrounds (see Fig. 5). **(C, D)** Similar results from condition 3, with saccades crossing a luminance edge. The black curves in this case are the same as in **A**, **B**. All other conventions are similar to Figs. 4, 5.

Perceptual suppression occurs equally well, and with the same visual dependencies, for image sweeps that conceptually mimic saccade-induced image shifts

The above evidence is indicative of strong and rich visual-visual interactions in saccadic suppression between the saccade-related retinal image shifts and the probe flashes themselves, as we have recently suggested (Idrees, Baumann, Franke, et al., 2020; Idrees, Baumann, Korympidou, et al., 2020). If that is indeed the case, then the same visual dependencies as those demonstrated in Figs. 3-6 should also happen in

28

853   the complete absence of saccades, but in the presence of saccade-like image shifts

854   and probe flashes. We therefore repeated the above experiments but with so-called

855   "simulated saccades". We asked subjects to fixate, and we swept a vertical

856   luminance-defined edge across the retina to simulate a saccade-like image

857   displacement (Fig. 2A). This condition was therefore conceptually similar to condition

858   3 (Methods). The probe flashes happened identically to how they happened in the

859   real saccade version of the experiment; that is, they occurred over a dark or bright

860   background, and they also had either positive (luminance increment) or negative

861   (luminance decrement) stimulus polarity. We also additionally tested pre-shift probe

862   flashes, to check for perceptual suppression before "simulated saccade" onset

863   (Idrees, Baumann, Franke, et al., 2020).

864

865   We replicated all of the above observations that were made with real saccades. First,

866   we confirmed that immediately after saccade-like image translation, strong

867   perceptual suppression occurred, which was much stronger than the suppression

868   with real saccades across a uniform background. This effect is demonstrated in Fig.

869   7A, which shows the average psychometric curve across all subjects when a

870   negative polarity flash appeared over a dark background at 47 ms after image

871   translation onset (magenta curve). For reference, the black curve in the same figure

872   shows the average psychometric curve associated with "real" saccadic suppression

873   over a uniform (dark) background at our shortest flash time (i.e. associated with

874   maximal saccadic suppression in our data set). As can be seen, perceptual

875   thresholds were strongly elevated even with the simulated saccades, just like in

876   condition 3. Across flash times, Fig. 7B shows that immediately after image shift

877   onset, the absolute value of threshold contrast over a dark background was 0.54

878   Weber contrast for negative polarity flashes. This value was much higher than that

879   for real saccades across uniform backgrounds (0.13 Weber contrast for the shortest

880   flash time with the real saccade; 40 ms). Statistically, we confirmed this by doing a

881   paired comparison of thresholds between condition 4 (0.54 +/- 0.11 s.e.m. Weber

882   contrast) and condition 1 (0.13 +/- 0.02 s.e.m. Weber contrast) at the shortest

883   positive flash time after either image translation onset or saccade onset (t(5) = 4.7, p
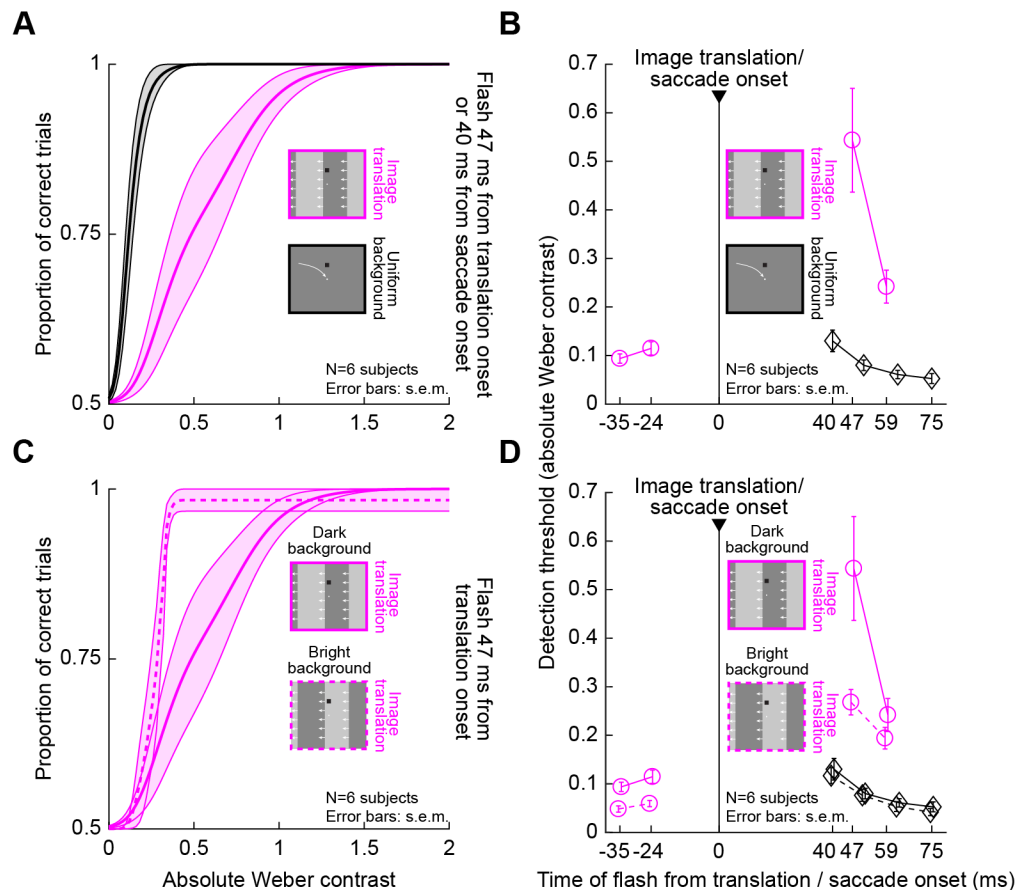
884   = 0.005).

885

886

29

Figure 7 Highly similar visual dependencies of perceptual suppression in the absence of saccades. (A) Psychometric curve of perceptual detectability from condition 4, in which a saccade-like displacement of a vertical luminance edge took place (conceptually similar to condition 3 with real saccades). For reference, the black curve shows the psychometric curve from condition 1 (real saccades over a uniform background) at 40 ms. The saccade-like image displacement caused large suppression (a larger rightward shift of the curve), similar to the large suppression seen with real saccades (e.g. Fig. 4). Error bands denote s.e.m. across subjects. **(B)** Time course of perceptual suppression in condition 4. For reference, the time course of saccadic suppression over a uniform background (condition 1) is also shown in black. **(C)** There was also stronger suppression with (negative polarity) flashes over a dark background than with the same flashes over a bright background, exactly like with real saccades (e.g. Fig. 5). The average psychometric curve was shifted more to the right with a dark background (solid). **(D)** The dependence of perceptual suppression on background luminance was also clear in the whole time course, and this dependence was similar to that seen with real saccades in a similar visual condition of crossing an edge (e.g. Fig. 5). For reference, the black curves show the results obtained with real saccades across a uniform dark (solid) or bright (dashed) background (same as in Fig. 6).

Second, we confirmed that there was stronger perceptual suppression over a dark background versus over a bright background with our simulated saccades of condition 4. This effect can be seen in Fig. 7C, in which we plotted the average psychometric curves across all subjects at the same flash time, but with flashes occurring over either a bright or dark background. As we did above for simplicity in several other figures, we only plotted the curves for negative polarity flashes (but see below for explicit analysis of flash polarity in this condition as well). As can be seen,

30

913   the psychometric curve for dark backgrounds (replicated from Fig. 7A) was shifted

914   farther to the right compared to the curve for bright backgrounds, consistent with

915   stronger perceptual suppression. In Fig. 7D, the full time courses can be seen for

916   both background luminances. For reference, the curves for saccadic suppression

917   with real saccades over a uniform background are also shown in black (condition 1).

918   At the first time point after visual transient onset in the simulated saccade condition,

919   threshold contrast was 0.54 +/- 0.11 s.e.m. and 0.27 +/- 0.03 s.e.m. Weber contrast

920   for dark and bright backgrounds, respectively (paired t-test: $t(5) = 4.5$, $p = 0.006$).

921

922   Finally, we also confirmed that the same interactions between flash polarity and

923   background luminance also persisted with simulated saccade-like image shifts.

924   Specifically, we used condition 4 to explore psychometric curves of perceptual

925   detectability when flashes appeared at different times relative to image displacement

926   onset and on different background luminances. Figure 8A shows such curves for the

927   case of negative or positive polarity flashes appearing over a dark background 47 ms

928   after the onset of rapid image displacement. The curve for the negative polarity

929   flashes was shifted more to the right than the curve for positive polarity flashes,

930   suggesting stronger perceptual suppression. This is similar to what we also saw with

931   real saccades (Fig. 6). Indeed, the time courses (Fig. 8B, C) exhibited very similar

932   dependencies on flash polarity to the real saccade conditions. For example, over a

933   dark background (Fig. 8B), perceptual thresholds were at 0.54 +/- 0.11 s.e.m. Weber

934   contrast for negative polarity flashes, and 0.35 +/- 0.04 s.e.m. for positive polarity

935   flashes, at the time closest to peak suppression in our data (47 ms). This was

936   statistically significant (paired t-test: $t(5) = 2.7$, $p = 0.04$). For reference, Fig. 8B also

937   shows the thresholds from condition 1 with real saccades over a uniform background.

938   As can be seen, the suppression was significantly stronger with translation of a

939   luminance edge across the retina than with real saccades over a uniform

940   background. In fact, the threshold values in condition 4 (Figs. 7, 8) immediately after

941   simulated saccade onset were generally similar in strength to those obtained

942   immediately after real saccades in condition 3 (e.g. Figs. 4, 5); however, we caution

943   against direct quantitative comparison, especially given the very different time

944   courses of real versus simulated saccadic suppression profiles that can exist (Idrees,

945   Baumann, Franke, et al., 2020).

946

947   The interaction between flash polarity and background luminance also extended to

948   bright backgrounds. Specifically, with real saccades in conditions 2 and 3, we saw

949   above (Fig. 6) that flash polarity did not alter saccadic suppression strength when

950   flashes appeared over a bright background, unlike the case with flashes occurring

951   over a dark background. This happened in a similar way in condition 4 with simulated

952   saccades (Fig. 8C). Therefore, all of the visual dependencies that we observed with

953   real saccades (Figs. 3-6) also occurred in the absence of any saccades, when

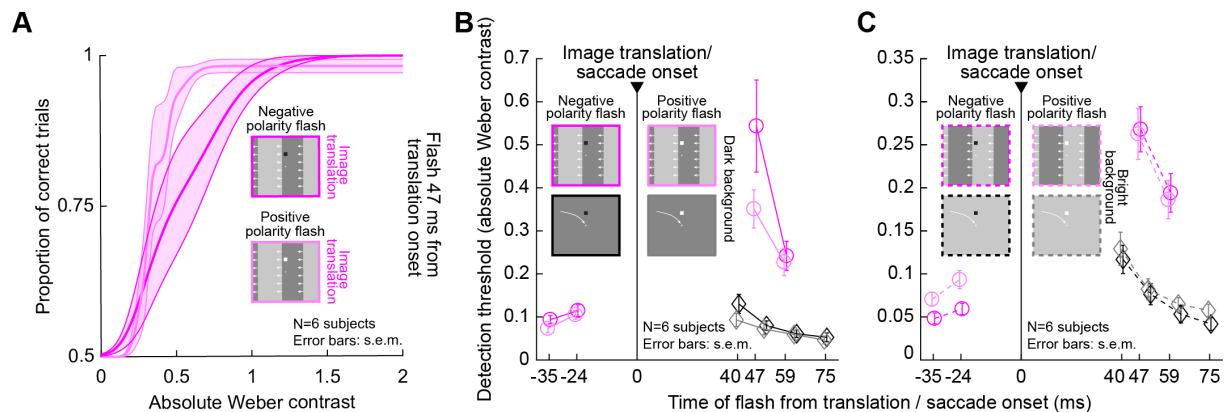954   saccade-like image translations were introduced (Figs. 7, 8).

955

956

957

958

959 **Figure 8 Stronger suppression for negative polarity flashes over dark backgrounds when**
960 **compared to positive polarity flashes, even in the absence of saccades. (A)** Average psychometric
961 curves for negative and positive polarity flashes occurring at 47 ms after image translation onset, and
962 appearing over a dark background. Saturated colors show results with negative polarity flashes, and
963 unsaturated colors show results with positive polarity flashes. Error bands denote s.e.m. across
964 subjects. Negative polarity flashes were associated with stronger perceptual suppression than positive
965 polarity flashes. **(B)** Perceptual thresholds across subjects as a function of flash time after image
966 translation onset in condition 4, comparing negative and positive polarity flashes over a dark background
967 (error bars denote s.e.m. across subjects). For reference, the time course of suppression from condition
968 1 is also shown in black. Consistent with Fig. 7, perceptual suppression with an image translation
969 (condition 4) was much stronger (higher perceptual thresholds) than in condition 1 with real saccades
970 (compare colored to black curves). Moreover, perceptual saccadic suppression was stronger with
971 negative polarity flashes than positive polarity flashes, especially near the time of peak suppression (47
972 ms). This is identical to the effect that we saw with real saccades in Fig. 6. **(C)** With bright backgrounds,
973 the effects of flash polarity were absent, again consistent with what we observed with real saccades
974 (Fig. 6).

975

976

977

978   It should be noted here that our simulated saccade condition was also important

979   because it allowed us to additionally test probe flashes occurring before simulated

980   saccade onset. In Figs. 7, 8, flashes with negative time were presented before the

981   image translation. Nonetheless, they were still associated with threshold elevations,

982   as we also recently reported in similar experiments (Idrees, Baumann, Franke, et al.,

983   2020). For example, in Fig. 7B, perceptual threshold for a flash time of -24 ms was

984   0.11 Weber contrast, whereas it was only 0.09 at -35 ms. Therefore, there was

985   elevation of threshold as time approached the onset of the image translation. These

986   results, combined with earlier published work in the literature, make it likely that we

987   would also observe pre-saccadic suppression in conditions 1, 2, and 3 above if we

988   were to present flashes before the real saccades. Interestingly, even pre-translation

989   flashes were clearly associated with stronger suppression when they occurred over a

990   dark background as opposed to a bright background (Fig. 7D), consistent with the

991   post-translation flash times demonstrating an influence of background luminance,

992   which are in turn consistent with real saccade background effects.

993

994

995   *Luminance steps without saccade-like image sweeps cause modest perceptual*

996   *suppression*

997   Finally, for completeness, we also tested simple luminance steps during fixation, with

998   no image translations (condition 5; Methods). In this case, we previously found that

999   perceptual suppression does occur (Idrees, Baumann, Franke, et al., 2020), although

1000   in that previous study, we did not explore certain factors, like flash polarity, in much

1001   detail.

1002

1003   With luminance steps, perceptual suppression was significantly weaker in strength

1004   than with an image translations. For example, Fig. 9A shows thresholds when a flash

1005   occurred over a dark background, and Fig. 9B shows thresholds when a flash

1006   occurred over a bright background. For reference, saccadic suppression thresholds

1007   from condition 1 (i.e. with saccades across a uniform background) are also shown in

1008   black. Both conditions had the weakest overall suppression strengths in the whole

1009   study, and peak suppression in them was very similar. For example, at the first flash

1010   time after contrast change or saccade onset, the overall thresholds in both conditions

1011   were less than 0.18 Weber contrast (Fig. 9), which is much less than threshold

1012   contrasts in all other experiments with luminance edges or stripes (whether with or

1013   without saccades). This suggests an interesting role of luminance transients over

1014   peri-foveal image regions in perceptual saccadic suppression. Specifically, peri-

1015   foveally, the uniformity of the display was similar during the real saccades (condition

1016 1) and the contrast change experiment (condition 5); both conditions were lacking

1017 local image translation across the retinal regions that were also probed with brief

1018 flash stimuli. Even though the entire retinal image (including display outer edges)

1019 were translated across the retina during real saccades, it seems that such a local

1020 image translation is necessary to maximize perceptual suppression of temporally-

1021 close probe flashes.
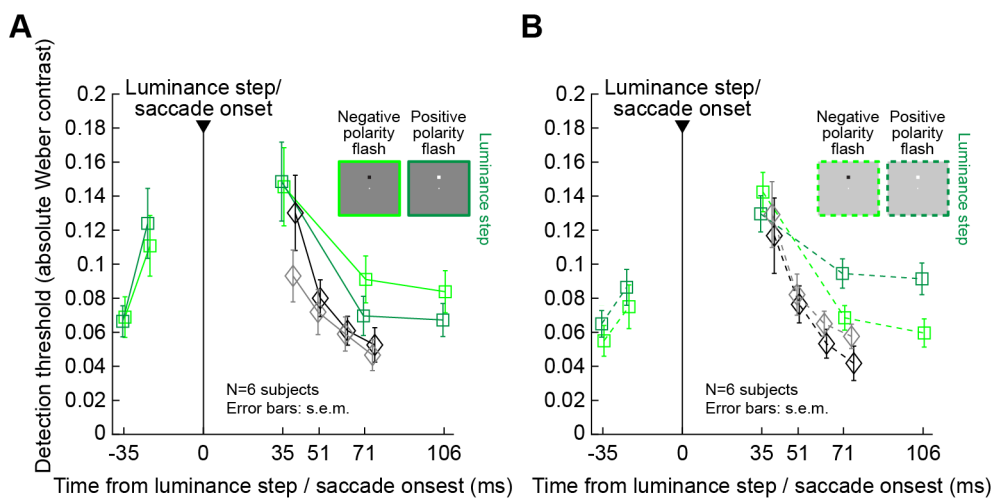
1022

1023

1024

1025

1026 **Figure 9 Weak perceptual suppression with simple luminance steps during fixation. (A)**
1027 Perceptual contrast thresholds from condition 5 with just luminance steps (colored curves). Each curve
1028 shows results for either a positive (dark green) or negative (light green) polarity flash over a dark
1029 background, and error bars denote s.e.m. across subjects. For reference, thresholds from condition 1
1030 are shown in black. Peak suppression with a luminance step was as weak as the suppression with real
1031 saccades over a uniform background (this was our weakest suppression condition in all experiments;
1032 Figs. 1-8). Moreover, during recovery, negative polarity flashes were harder to detect than positive
1033 polarity flashes. **(B)** Similar results for flashes occurring over a bright background. Now, it was positive
1034 polarity flashes that were harder to detect than negative polarity flashes during the recovery phase (at
1035 times 71 and 106 ms after luminance step occurrence). All other conventions are similar to Figs. 4, 5.

1036

1037

1038

1039

1040 Figure 9 also reveals interesting differential effects of flash polarity on perceptual

1041 thresholds, but only at longer times after contrast change. Specifically, at both 71 ms

1042 and 106 ms after background luminance change (from bright to dark or vice versa),

1043 there was an interaction between flash polarity and background luminance: negative

1044 polarity flashes were harder to detect compared to positive polarity flashes over dark

1045 backgrounds, whereas positive polarity flashes over bright backgrounds were harder

1046 to detect than negative polarity flashes. To statistically validate this, we pooled the

34

1047   two latest flash times together and compared, with a paired t-test for each

1048   background, whether the detection thresholds differed for the two flash polarities.

1049   With a dark background, the positive polarity (mean threshold: 0.07 +/- 0.01 s.e.m.

1050   Weber contrast) significantly differed from the negative polarity (mean threshold: 0.09

1051   +/- 0.01 s.e.m.) (t(5) = 5.8, p = 0.0022). Over a bright background, the positive

1052   polarity (threshold: 0.09 +/- 0.01 s.e.m. Weber contrast) significantly differed from the

1053   negative polarity (0.06 +/- 0.01 s.e.m.) (t(5) = -16, p <10^{-4}). This effect was not

1054   present in any of our real or simulated saccade conditions (conditions 1-4), and it

1055   also might be a simple instantiation of Weber's law, irrespective of perceptual

1056   suppression. Interestingly, in our recent investigation of a similar perceptual

1057   paradigm (Idrees, Baumann, Korympidou, et al., 2020), there was no clear impact of

1058   flash polarity. However, in that study, we did not use the more sensitive psychometric

1059   approach that we used here, so we could have been affected by floor and ceiling

1060   effects in that earlier study. Nonetheless, it is interesting that visual-visual

1061   interactions in saccadic suppression are best matched under fixation when saccade-

1062   like image displacements take place; other transients, such as just simple

1063   background luminance steps (Fig. 9), also cause mild suppression, but with different

1064   visual dependencies.

1065

1066

1067   **Discussion**

1068

1069   We investigated the visual components of perceptual saccadic suppression. We

1070   collected psychometric curves of perceptual detectability for brief peri-saccadic

1071   flashes and used these curves to estimate thresholds. We found that perceptual

1072   thresholds were only elevated mildly when saccades were made across a uniform

1073   background, but they were dramatically increased when gaze crossed a luminance

1074   edge (e.g. Figs. 3, 4). Moreover, the luminance at which gaze landed after saccade

1075   end did not have to be different to the luminance at saccade onset for the strength of

1076   saccadic suppression to increase; crossing a luminance stripe was also associated

1077   with very strong saccadic suppression when compared to the uniform background

1078   (condition, 2, e.g. Fig. 4). Interestingly, saccadic suppression was the strongest

1079   when the luminance of the background was dark, and there was an impact of flash

1080   polarity relative to the background luminance (particularly with negative polarity

1081   flashes over dark backgrounds; e.g. Figs. 5, 6). Critically, all of these visual

1082   dependencies of saccadic suppression still occurred when we replaced saccades

1083   with image displacements in the absence of any saccadic eye movements (e.g. Figs.

1084   7, 8).

1085

1086   Our results from condition 3 confirm and extend those of (Maij et al., 2012).

1087   Specifically, in that study, the authors used a condition similar to ours (Fig. 1A,

1088   bottom), and they asked subjects to indicate whether they missed seeing a peri-

1089   saccadic flash or not (the overall context of the task was to study mislocalization of

1090   observed flash location, so the flashes were supra-threshold in general compared to

1091   ours). When the saccades were made over a uniform background, the subjects

1092   almost never missed the flashes. However, when the saccades involved gaze

1093   crossing a vertical luminance edge, there was an increased likelihood of misses. This

1094   is also what we saw with our more sensitive threshold measurements in the current

1095   study (e.g. Figs. 3, 4). As stated above, we also saw almost equally strong

1096   suppression when the edge was replaced with just a luminance stripe (condition 2,

1097   i.e. the starting and landing gaze positions were on the same background luminance;

1098   Figs. 3, 4). Combined, these results suggest that visual-visual interactions, in the

1099   form of gaze crossing a luminance pattern, matter a great deal for saccadic

1100   suppression.

1101

1102   Moreover, the effects are highly repeatable across individuals. In all analyses,

1103   average measurements across subjects were very consistent and repeatable, as

1104   evidenced by the small error bars in all our figures. Indeed, when we plotted the

1105   individual psychometric curves of each subject for one of the conditions, as in the

1106   example of Fig. 10, we saw remarkable repeatability across subjects. This was true

1107   in our earlier study as well, in which we saw high consistency across individual

1108   subjects (Idrees, Baumann, Franke, et al., 2020). Therefore, the effects that we

1109   report here are clearly robust across individuals.
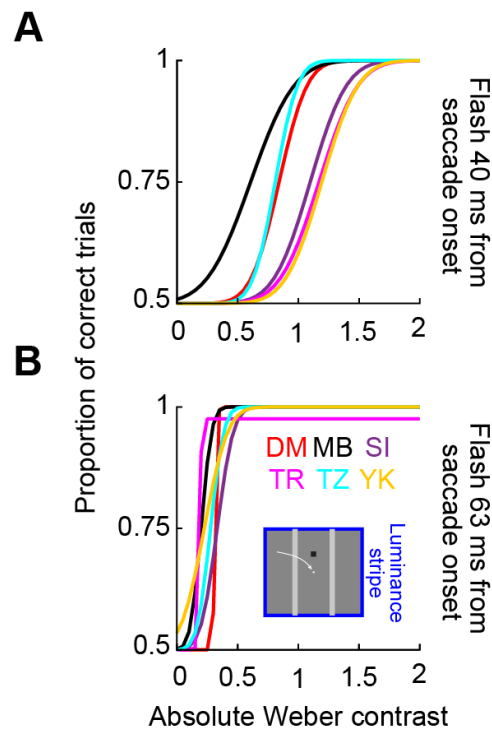
1110

1111

1112

1113   **Figure 10 Raw psychometric curves at two flash times from each individual subject in condition
1114   2. (A)** Psychometric curves of all subjects with a negative polarity flash at 40 ms and dark backgrounds.
1115   **(B)** The same for the flash at 63 ms. There was strong coherence across subjects in the modulations of
1116   perceptual detectability in our experiments.

1117

1118

1119

1120   It is also interesting that the background luminance has a strong influence on the

1121   strength of saccadic suppression. In all analyses, we assessed perceptual thresholds

1122   based on calculating the absolute luminance difference between the probe flash and

1123   the background, normalized against the background luminance (i.e. Weber contrast).

1124   We observed that subjects needed more luminance contrast relative to the

37

1125   background (even with positive polarity flashes) to detect stimuli peri-saccadically (or

1126   peri-translation in condition 4) when the overall background was dark than when it

1127   was light. The fact that this effect was stronger with the dark background compared

1128   to the bright one rules out the possibility that this was a simple instantiation of basic

1129   Weber's law (i.e. that more luminance needs to be added to a bright background than

1130   to a dark background for equal detectability). Rather, there was an apparent

1131   interaction between image translation and gaze finally encountering an image patch

1132   with a dark region. Similarly, there was also an interaction associated with the probe

1133   polarity itself: after saccades (or image translations), dark backgrounds required

1134   larger negative polarity contrasts for perceptual detection than positive polarity

1135   contrasts, but no polarity effects existed with a bright background (e.g. Fig. 6). It

1136   could be the case that crossing an image patch to a darker background induces a

1137   stronger visual transient (e.g. in the retina) than crossing an image patch to a brighter

1138   background, which then modifies the subsequent visual response to the probe flash

1139   itself. It would be interesting to explore this mechanism by relating how our observed

1140   interaction effects (that is, perceptually) relate to the activity of ON and OFF channels

1141   in ex-vivo mouse and pig retinae, similar to our recent investigations (Idrees,

1142   Baumann, Korympidou, et al., 2020). Intriguingly, preliminary data from that study

1143   indicate that ex-vivo non-human primate retinae may exhibit ON and OFF

1144   dependencies that might be similar to human effects (Idrees, Baumann, Korympidou,

1145   et al., 2020), at least in our condition 5. On the other hand, our probe flash polarity

1146   effects (e.g. Figs. 6, 8) demonstrate that strong perceptual suppression can occur

1147   irrespective of the combination of visual transient polarity and probe flash polarity;

1148   this suggests the presence of other suppressive mechanisms beyond the dynamic

1149   reversal suppression mechanism (which depends on a difference in polarity between

1150   visual transient and probe flash) that we uncovered in the mouse and pig retinae in

1151   the same study. Of course, it would also be interesting to investigate the visual-visual

1152   interactions of saccadic suppression in neural circuits downstream of the retina in

1153   non-human primates (or other relevant species used in systems neuroscience).

1154

1155   The importance of visual-visual interactions in perceptual saccadic suppression also

1156   makes us consider the possibility that with our uniform background condition

1157   (condition 1), the edges of the monitor may have had a non-negligible modulatory

1158   effect on the phenomenon. Specifically, for both the bright and dark background

1159   luminances used in the uniform background condition, the display monitor was still

1160   brighter than the rest of the laboratory. Therefore, there was a rectangular frame that

1161   was moved on the retina by the saccades. This likely affected perception since our

1162   other conditions (with luminance edges crossing the fovea) had a very strong effect

1163   on the strength of saccadic suppression. Nonetheless, it is still intriguing that, by far,

1164   the largest effects on peri-saccadic perceptual thresholds that we observed required

1165   that the luminance edges or patterns cross the fovea during the saccades. Such

1166   foveal crossing (or, more generally, crossing of the retinal patch experiencing the

1167   probe flashes) also happened in our simulated saccade condition (condition 4), which

1168   again showed strong perceptual suppression effects. This could be a function of the

1169   spatial resolution of the retinal regions (and associated downstream visual areas)

1170   that experience temporal luminance modulations during the saccades and the

1171   flashes.

1172

1173   In addition to the above effects in real saccades, we also saw essentially the same

1174   visual dependencies in experiments with visual-visual interactions no longer involving

1175   real saccades. Specifically, in our condition 4, we translated the luminance edge

1176   across the fovea and presented probe flashes near the time of the translation. We

1177   observed the same dependencies on background luminance, and the same

1178   interactions with flash luminance polarity, as with real saccades. This confirms our

1179   hypothesis (Idrees, Baumann, Franke, et al., 2020; Idrees, Baumann, Korympidou, et

1180   al., 2020) that visual-visual interactions play an important role in saccadic

1181   suppression, and it also extends the image conditions under which we could observe

1182   remarkable similarities between real and simulated saccades in terms of perceptual

1183   suppression (Idrees, Baumann, Franke, et al., 2020). All of this is in agreement with

1184   other phenomena, like the fact that intra-saccadic motion can still be perceived if its

1185   speed is within the detectability range of our motion sensors in the brain (Castet et

1186   al., 2001; Castet & Masson, 2000), and also the fact that intra-saccadic motion

1187   streaks provide important reference frames for keeping track of object locations

1188   (Schweitzer & Rolfs, 2020). This evidence highlights the role of vision even during

1189   rapid eye movements. In that sense, suppression occurring before saccades or

1190   image translations (e.g. Figs. 7-9) may be viewed as reflecting visual-visual

1191   interactions such as backwards masking (Breitmeyer, 2007; Brooks & Fuchs, 1975;

1192   Judge, Wurtz, & Richmond, 1980; Mackay, 1970; Mitrani et al., 1975).

1193

1194   Naturally, a role for prior knowledge of movement commands at the time of saccade

1195   generation (e.g. corollary discharge) must additionally matter for saccadic

1196   suppression, and the real question becomes how visual and non-visual mechanisms

1197   interact in this phenomenon. In other words, it need not be the case that saccadic

1198   suppression is only purely motor or only purely visual. For example, experiments

1199   under conditions of whiteout (i.e. absolutely uniform illumination across the entire

1200   retina) might suggest a role for a movement-related impact on perceptual saccadic

1201   suppression (Riggs & Manning, 1982). Interestingly, at the neural level,

1202   enhancement, rather than suppression, seems to take place in human LGN and V1

1203   across saccades without visual stimulation (Sylvester, Haynes, & Rees, 2005;

1204   Sylvester & Rees, 2006). This suggests a very different role for knowledge of

1205   saccade commands than simply to actively reduce visual sensitivity. Similarly, we

1206   recently found that while the visual properties of perceptual suppression were highly

1207   similar with or without real saccades, there was a massive difference in the time

1208   course of suppression when real saccades were generated: perceptual suppression

1209   was much more short-lived when it was associated with real saccades than when it

1210   was triggered by visual-visual interactions in the absence of saccades (Idrees,

1211   Baumann, Franke, et al., 2020). This is very reassuring, in retrospect, because of the

1212   strong need to minimize saccade-induced disruptions in vision as much as possible.

1213   However, it also raises highly interesting and unanswered questions on what exactly

1214   the role of saccade-related movement commands is in modulating the properties of

1215   perceptual saccadic suppression. Could it be that corollary discharge is there to

1216   shorten saccadic suppression, rather than to cause it? This is a topic that we think

1217   will lead to very interesting new neurophysiological insights on the field of trans-

1218   saccadic perception.

1219

1220

1221   **Conclusions**

1222

1223   The phenomenon of perceptual saccadic suppression possesses a strong visual

1224   component, reflecting interactions between visual activation caused by saccade-

1225   induced image translations and visual activation caused by the brief probe flashes

1226   used to measure the sensitivity of the visual system around the time of saccades.

1227   This visual component of saccadic suppression motivates future neurophysiological,

1228   perceptual, and theoretical investigations on how this component interacts with

1229   internal knowledge of saccadic movement generation commands (i.e. efference

1230   copies or corollary discharge) for minimizing the disruptions to vision that can be

1231   caused by saccades.

1232

1233

1234 **Acknowledgements**

1235

1239

1240

1241

1242

References

1244

1245 Adey, W. R., & Noda, H. (1973). Influence of eye movements on geniculo-striate excitability
1246   in the cat. *J Physiol, 235*(3), 805-821. doi:10.1113/jphysiol.1973.sp010418
1247 Beeler, G. W., Jr. (1967). Visual threshold changes resulting from spontaneous saccadic eye
1248   movements. *Vision Res, 7*(9), 769-775.
1249 Bellet, J., Chen, C. Y., & Hafed, Z. M. (2017). Sequential hemifield gating of alpha- and beta-
1250   behavioral performance oscillations after microsaccades. *J Neurophysiol, 118*(5),
1251   2789-2805. doi:10.1152/jn.00253.2017
1252 Bellet, M. E., Bellet, J., Nienborg, H., Hafed, Z. M., & Berens, P. (2019). Human-level saccade
1253   detection performance using deep neural networks. *J Neurophysiol, 121*(2), 646-661.
1254   doi:10.1152/jn.00601.2018
1255 Benedetto, A., & Morrone, M. C. (2017). Saccadic Suppression Is Embedded Within Extended
1256   Oscillatory Modulation of Sensitivity. *J Neurosci, 37*(13), 3661-3670.
1257   doi:10.1523/JNEUROSCI.2390-16.2016
1258 Berman, R. A., Cavanaugh, J., McAlonan, K., & Wurtz, R. H. (2017). A circuit for saccadic
1259   suppression in the primate brain. *J Neurophysiol, 117*(4), 1720-1735.
1260   doi:10.1152/jn.00679.2016
1261 Binda, P., & Morrone, M. C. (2018). Vision During Saccadic Eye Movements. *Annu Rev Vis Sci,
1262   4*, 193-213. doi:10.1146/annurev-vision-091517-034317
1263 Bogadhi, A. R., Buonocore, A., & Hafed, Z. M. (2020). Task-irrelevant visual forms facilitate
1264   covert and overt spatial selection. *J Neurosci*. doi:10.1523/JNEUROSCI.1593-20.2020
1265 Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial vision, 10*(4), 433-436.
1266 Breitmeyer, B. G. (2007). Visual masking: past accomplishments, present status, future
1267   developments. *Advances in Cognitive Psychology, 3*(1), 9-20.
1268 Bremmer, F., Kubischik, M., Hoffmann, K. P., & Krekelberg, B. (2009). Neural dynamics of
1269   saccadic suppression. *J Neurosci, 29*(40), 12374-12383. doi:29/40/12374 [pii]
1270 10.1523/JNEUROSCI.2908-09.2009
1271 Brooks, B. A., & Fuchs, A. F. (1975). Influence of stimulus parameters on visual sensitivity
1272   during saccadic eye movement. *Vision Res, 15*(12), 1389-1398. doi:10.1016/0042-
1273   6989(75)90196-0
1274 Brooks, B. A., Impelman, D. M., & Lum, J. T. (1981). Backward and forward masking
1275   associated with saccadic eye movement. *Percept Psychophys, 30*(1), 62-70.
1276 Burr, D. C., Morrone, M. C., & Ross, J. (1994). Selective suppression of the magnocellular
1277   visual pathway during saccadic eye movements. *Nature, 371*(6497), 511-513.
1278   doi:10.1038/371511a0
1279 Castet, E., Jeanjean, S., & Masson, G. S. (2001). 'Saccadic suppression'- no need for an active
1280   extra-retinal mechanism. *Trends Neurosci, 24*(6), 316-318.
1281 Castet, E., & Masson, G. S. (2000). Motion perception during saccadic eye movements. *Nat
1282   Neurosci, 3*(2), 177-183. doi:10.1038/72124
1283 Chen, C. Y., & Hafed, Z. M. (2013). Postmicrosaccadic enhancement of slow eye movements.
1284   *The Journal of neuroscience : the official journal of the Society for Neuroscience,
1285   33*(12), 5375-5386. doi:10.1523/JNEUROSCI.3703-12.2013

1286   Chen, C. Y., & Hafed, Z. M. (2017). A neural locus for spatial-frequency specific saccadic
1287   suppression in visual-motor neurons of the primate superior colliculus. *J*
1288   *Neurophysiol, 117*(4), 1657-1673. doi:10.1152/jn.00911.2016
1289   Chen, C. Y., Ignashchenkova, A., Thier, P., & Hafed, Z. M. (2015). Neuronal Response Gain
1290   Enhancement prior to Microsaccades. *Curr Biol, 25*(16), 2065-2074.
1291   doi:10.1016/j.cub.2015.06.022
1292   Cornelissen, F. W., Peters, E. M., & Palmer, J. (2002). The Eyelink Toolbox: eye tracking with
1293   MATLAB and the Psychophysics Toolbox. *Behavior research methods, instruments, &*
1294   *computers : a journal of the Psychonomic Society, Inc, 34*(4), 613-617.
1295   doi:10.3758/bf03195489
1296   DeYoe, E. A., & Van Essen, D. C. (1988). Concurrent processing streams in monkey visual
1297   cortex. *Trends Neurosci, 11*(5), 219-226. doi:10.1016/0166-2236(88)90130-0
1298   Diamond, M. R., Ross, J., & Morrone, M. C. (2000). Extraretinal control of saccadic
1299   suppression. *J Neurosci, 20*(9), 3449-3455.
1300   Duffy, F. H., & Lombroso, C. T. (1968). Electrophysiological evidence for visual suppression
1301   prior to the onset of a voluntary saccadic eye movement. *Nature, 218*(5146), 1074-
1302   1075. doi:10.1038/2181074a0
1303   Gremmler, S., & Lappe, M. (2017). Saccadic suppression during voluntary versus reactive
1304   saccades. *J Vis, 17*(8), 8. doi:10.1167/17.8.8
1305   Hafed, Z. M. (2013). Alteration of visual perception prior to microsaccades. *Neuron, 77*(4),
1306   775-786. doi:10.1016/j.neuron.2012.12.014
1307   Hafed, Z. M., Chen, C.-Y., & Tian, X. (2015). Vision, perception, and attention through the
1308   lens of microsaccades: mechanisms and implications. *Front Syst Neurosci, 9*, 167.
1309   doi:10.3389/fnsys.2015.00167
1310   Hafed, Z. M., & Krauzlis, R. J. (2010). Microsaccadic suppression of visual bursts in the
1311   primate superior colliculus. *J Neurosci, 30*(28), 9542-9547. doi:30/28/9542 [pii]
1312   10.1523/JNEUROSCI.1137-10.2010
1313   Idrees, S., Baumann, M. P., Franke, F., Munch, T. A., & Hafed, Z. M. (2020). Perceptual
1314   saccadic suppression starts in the retina. *Nature communications, 11*(1), 1977.
1315   doi:10.1038/s41467-020-15890-w
1316   Idrees, S., Baumann, M. P., Korympidou, M. M., Schubert, T., Kling, A., Franke, K., . . . Munch,
1317   T. A. (2020). Suppression without inhibition: A novel mechanism in the retina
1318   accounts for saccadic suppression. *bioRxiv*. doi:10.1101/2020.08.21.261198
1319   Judge, S. J., Wurtz, R. H., & Richmond, B. J. (1980). Vision during saccadic eye movements. I.
1320   Visual interactions in striate cortex. *J Neurophysiol, 43*(4), 1133-1155.
1321   Kagan, I., Gur, M., & Snodderly, D. M. (2008). Saccades and drifts differentially modulate
1322   neuronal activity in V1: effects of retinal image motion, position, and extraretinal
1323   influences. *J Vis, 8*(14), 19 11-25. doi:10.1167/8.14.19
1324   /8/14/19/ [pii]
1325   Kleiner, M., Brainard, D., & Pelli, D. G. (2007). What's new in Psychtoolbox-3? (Abstract).
1326   *Perception, 36*.
1327   Latour, P. L. (1962). Visual threshold during eye movements. *Vision Res, 2*(3), 261-262.
1328   Mackay, D. M. (1970). Elevation of visual threshold by displacement of retinal image. *Nature,*
1329   *225*(5227), 90-92. doi:10.1038/225090a0
1330   Maij, F., Matziridi, M., Smeets, J. B., & Brenner, E. (2012). Luminance contrast in the
1331   background makes flashes harder to detect during saccades. *Vision Res, 60*, 22-27.
1332   doi:10.1016/j.visres.2012.03.003

1333 Matin, E. (1974). Saccadic suppression: a review and an analysis. *Psychol Bull, 81*(12), 899-
1334   917.
1335 Melcher, D. (2011). Visual stability. *Philos Trans R Soc Lond B Biol Sci, 366*(1564), 468-475.
1336   doi:10.1098/rstb.2010.0277
1337 Merigan, W. H., & Maunsell, J. H. (1993). How parallel are the primate visual pathways?
1338   *Annu Rev Neurosci, 16*, 369-402. doi:10.1146/annurev.ne.16.030193.002101
1339 Mitrani, L., Mateeff, S., & Yakimoff, N. (1971). Is Saccadic Suppression Really Saccadic. *Vision*
1340   *Research, 11*(10), 1157-+. doi:Doi 10.1016/0042-6989(71)90119-2
1341 Mitrani, L., Radil-Weiss, T., Yakimoff, N., Mateeff, S., & Bozkov, V. (1975). Various
1342   background pattern-effect on saccadic suppression. *Act Nerv Super (Praha), 17*(3),
1343   161-164.
1344 Mitrani, L., Yakimoff, N., & Mateeff, S. (1973). Saccadic suppression in the presence of
1345   structured background. *Vision Res, 13*(2), 517-521.
1346 Noda, H., & Adey, W. R. (1974). Retinal ganglion cells of the cat transfer information on
1347   saccadic eye movement and quick target motion. *Brain Res, 70*(2), 340-345.
1348   doi:10.1016/0006-8993(74)90323-0
1349 Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: transforming
1350   numbers into movies. *Spatial vision, 10*(4), 437-442.
1351 Reppas, J. B., Usrey, W. M., & Reid, R. C. (2002). Saccadic eye movements modulate visual
1352   responses in the lateral geniculate nucleus. *Neuron, 35*(5), 961-974.
1353   doi:S0896627302008231 [pii]
1354 Riggs, L. A., & Manning, K. A. (1982). Saccadic suppression under conditions of whiteout.
1355   *Invest Ophthalmol Vis Sci, 23*(1), 138-143.
1356 Robinson, D. L., & Wurtz, R. H. (1976). Use of an extraretinal signal by monkey superior
1357   colliculus neurons to distinguish real from self-induced stimulus movement. *J*
1358   *Neurophysiol, 39*(4), 852-870.
1359 Ross, J., Morrone, M. C., Goldberg, M. E., & Burr, D. C. (2001). Changes in visual perception
1360   at the time of saccades. *Trends Neurosci, 24*(2), 113-121. doi:S0166-2236(00)01685-4
1361   [pii]
1362 Schutt, H. H., Harmeling, S., Macke, J. H., & Wichmann, F. A. (2016). Painfree and accurate
1363   Bayesian estimation of psychometric functions for (potentially) overdispersed data.
1364   *Vision Res, 122*, 105-123. doi:10.1016/j.visres.2016.02.002
1365 Schweitzer, R., & Rolfs, M. (2020). Intra-saccadic motion streaks as cues to linking object
1366   locations across saccades. *J Vis, 20*(4), 17. doi:10.1167/jov.20.4.17
1367 Sylvester, R., Haynes, J. D., & Rees, G. (2005). Saccades differentially modulate human LGN
1368   and V1 responses in the presence and absence of visual stimulation. *Curr Biol, 15*(1),
1369   37-41. doi:10.1016/j.cub.2004.12.061
1370 Sylvester, R., & Rees, G. (2006). Extraretinal saccadic signals in human LGN and early
1371   retinotopic cortex. *Neuroimage, 30*(1), 214-219.
1372   doi:10.1016/j.neuroimage.2005.09.014
1373 Watson, A. B., & Pelli, D. G. (1983). QUEST: a Bayesian adaptive psychometric method.
1374   *Percept Psychophys, 33*(2), 113-120.
1375 Wurtz, R. H. (2008). Neuronal mechanisms of visual stability. *Vision Res, 48*(20), 2070-2089.
1376   doi:S0042-6989(08)00172-7 [pii]
1377 10.1016/j.visres.2008.03.021
1378 Wurtz, R. H., Joiner, W. M., & Berman, R. A. (2011). Neuronal mechanisms for visual stability:
1379   progress and problems. *Philosophical transactions of the Royal Society of London.*
1380   *Series B, Biological sciences, 366*(1564), 492-503. doi:10.1098/rstb.2010.0186

1381   Yakimoff, N., Mitrani, L., & Mateeff, S. (1974). Saccadic suppression as visual masking effect.
1382   *Agressologie, 15*(6), 387-394.
1383   Zimmermann, E., & Bremmer, F. (2016). Visual Neuroscience: The Puzzle of Perceptual
1384   Stability. *Curr Biol, 26*(5), R199-201. doi:10.1016/j.cub.2016.01.050
1385   Zuber, B. L., & Stark, L. (1966). Saccadic suppression: elevation of visual threshold associated
1386   with saccadic eye movements. *Exp Neurol, 16*(1), 65-79. doi:0014-4886(66)90087-2
1387   [pii]
1388