1   # Red backgrounds have different effects on electrophysiological
2   # responses to fearful faces in groups with low and high autistic
3   # tendency

4   **Eveline Mu[1*], Laila Hugrass[2], David Crewther[1]**

5   [1]Centre for Human Psychopharmacology, Swinburne University of Technology
6   Melbourne, VIC, Australia
7   [2]School of Psychology and Public Health, La Trobe University, Melbourne, VIC, Australia

8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26

27   ***Corresponding author:**
28   Dr Eveline Mu
29   Centre for Human Psychopharmacology
30   Swinburne University of Technology
31   John St, Hawthorn VIC 3122
32   emu@swin.edu.au

Abstract

Visual processing differences in the magnocellular pathway have been reported across the autistic spectrum. On the basis that the firing of primate Type IV magnocellular cells is suppressed by diffuse red backgrounds, several groups have used red backgrounds as a means to investigate magnocellular contributions to visual processing in humans. Here, we measured emotional identification accuracy, and compared the P100 and N170 responses from groups with low (n=21; AQ<11) and high (n=22; AQ>22) Autism Spectrum Quotient (AQ) scores, in response to low (LSF) and high (HSF) spatially filtered fearful and neutral face stimuli presented on red and green backgrounds. For the LSF stimuli, the low AQ group correctly identified fearful expressions more often when presented on a red compared to a green background. The low AQ group also showed red backgrounds reduced the effect of LSF fearful expressions on P100 amplitudes. In contrast, the high AQ group showed that background colour did not significantly alter P100 responses to LSF stimuli. Interestingly, red background reduced the effects of HSF stimuli for the high AQ group. The effects of background color on LSF and HSF facial emotion responses were not evident for the N170 component. Our findings suggest that presenting face stimuli on a red background alters both magnocellular and parvocellular contributions to the P100 waveform, and that these effects differ for groups with low and high autistic tendencies. In addition, a theoretical model for explaining the temporal differences in facial emotion processing for low and high AQ groups is proposed.

1. Introduction

Rapid visual processing of fearful facial emotion is important for social functioning and for responding to potential threats in our environments . Facial emotion processing is impaired for individuals with autism spectrum disorder, and these impairments extend to the neurotypical population for groups with high versus low levels of autistic personality traits. Hence it is important to understand the neural basis of rapid facial emotion processing deficits for people with high levels of autistic personality traits. When viewing emotional faces, people with autism (Baron-Cohen et al., 2000; Corbett et al., 2009) and high levels of autistic traits tend to exhibit abnormal activation in amygdala (Nummenmaa et al., 2012), a subcortical region involved in affective processing. One proposal is that abnormalities in the rapidly conducting magnocellular pathways from the retina to the amygdala may underlie facial emotion processing deficits in the broader autistic phenotype (Burt et al., 2017).

Studies on the neural processing of emotional stimuli have implicated the amygdala as a crucial component in mediating such affective processing (Adolphs et al., 2001; Amaral et al., 2003; Batty & Taylor, 2003; Blau et al., 2007; LeDoux, 2003; Morris, 1998; Stein et al., 2014). The amygdala receives input via many visual processing routes, subcortical and cortical, with outputs distributed widely across occipital and parietal regions (Krolak-Salmon et al., 2004; Kveraga et al., 2007; Pessoa, 2010). The most prominent hypothesis regarding the rapid activation of the amygdala is the 'low road' hypothesis (LeDoux, 1996), which postulates that the initial analysis of threatening stimuli bypasses the visual cortex utilizing a rapid subcortical pathway projecting from the retina to the amygdala via the superior colliculus and pulvinar (with latencies of ~80ms) (Garvert et al., 2014; McFadyen et al., 2017; Morris et al., 1999; Tamietto et al., 2012). The alternative 'high road' geniculo-V1-amygdala pathway (Pessoa & Adolphs, 2010), demonstrates a latency of ~140ms (McFadyen et al., 2017; Silverstein & Ingvar, 2015), and recent anatomical research in primate has demonstrated a direct retina-pulvinar-amygdala pathway (Mundinano, 2019). However, there have been few investigations into how amygdala activation modulates cortical visual processing.

The magnocellular and parvocellular pathways work in parallel, processing low-level visual features. The magnocellular pathway is a fast-conducting stream that is insensitive to colour when the luminance is balanced, has higher contrast sensitivity, and is involved in transient attention, while the slower parvocellular pathway performs is colour sensitive, has lower contrast sensitivity, and is involved in sustained responses (Derrington & Lennie, 1984; Kaplan & Shapley, 1986; Laycock et al., 2007; Nassi & Callaway, 2009). It has also been shown

87   that the two early visual pathways are sensitive to different spatial frequencies, with the

88   magnocellular pathway being relatively sensitive to high temporal and low spatial frequency

89   (LSF) information, whilst the parvocellular pathway is more sensitive to low temporal and high

90   spatial frequency (HSF) information. Considering the evidence that fearful stimuli are rapidly

91   processed subcortically (Carr, 2015; Garvert et al., 2014; Johnson, 2005; Morris et al., 1999;

92   Öhman, 2005; Tamietto et al., 2012), it is plausible that this pathway processes coarse, LSF

93   information (Burt et al., 2017). This is consistent with findings that low pass filtered emotional

94   faces activate the amygdala more strongly than do high pass filtered faces (Vuilleumier et al.,

95   2003). This suggests that the magnocellular channels are responsible for driving the rapid salient

96   information to the amygdala. Some researchers (Burt et al., 2017; McCleery et al., 2007) have

97   proposed that less efficient inputs from the magnocellular pathway might contribute to

98   differences in face processing across the autistic personality spectrum.

99   Event related potentials (ERPs) from EEG recording have superior temporal resolution

100   compared with other brain imaging techniques such as fMRI and are highly effective in

101   identifying the timing of neural responses to emotional information. Two early ERP components

102   studied in affective research are the P100 and N170. The P100 represents a positive early peak

103   approximately 100ms post-stimulus onset. This peak reflects attentional gain (Hillyard & Anllo-

104   Vento, 1998), and seems to be more sensitive to low-level visual information (Mangun, 1995).

105   The N170 component is a negative deflection appearing approximately 170ms post-stimulus. It

106   reflects a structural and featural encoding phase in face processing (Mangun, 1995). The P100 is

107   recorded maximally over lateral occipital-parietal sites (Hillyard & Anllo-Vento, 1998), while

108   N170 originates from regions associated with face and object processing, such as the fusiform

109   gyrus, superior temporal sulcus and inferior, middle and superior temporal gyri (Henson et al.,

110   2003). Visual detection of fearful faces elicits a strong occipital-parietal peak as rapidly as 80ms

111   post-stimulus (Olivares et al. 2015) and 120-140ms post-stimulus (Eimer & Holmes, 2002;

112   Pourtois et al., 2004; Vlamings et al., 2009) compared to neutral faces. This suggests that the

113   amygdala may act as an early alerting mechanism which efficiently redirects visual attention to

114   the threatening stimuli derived from the fast-magnocellular route (Dumas et al., 2013; Ohman,

115   2005).

116   Considering magnocellular and parvocellular neurons respond preferentially to LSF and

117   HSF visual input, respectively (Benardete & Kaplan, 1999a, 1999b; Kaplan & Shapley, 1986), it is

118   likely that LSF and HSF filtered faces bias visual processing towards the magnocellular and

119   parvocellular routes, respectively. As such, previous electrophysiological evidence in typically

120   developing populations suggests that P100 amplitudes are greater in response to LSF fearful

4

121   expressions than to neutral expressions, but HSF emotional expressions do not modulate P100

122   amplitudes (Pourtois et al., 2005; Vlamings et al., 2009). Some studies have found effects of LSF

123   fearful expressions on N170 amplitudes (Vlamings et al., 2009), while others have not (Holmes et

124   al., 2005; Pourtois et al., 2005). A recent EEG study showed that for participants with low AQ

125   (Autism spectrum Quotient) scores, LSF fearful expressions have larger effects on P100 amplitudes

126   than HSF fearful expressions, yet for people with high AQ scores, fearful expressions tended not to

127   influence P100 amplitudes (Burt et al., 2017). This supports the notion that fearful face processing

128   deficits in ASD could be related to magnocellular pathway abnormalities in processing LSF visual

129   input (Corradi-Dell'Acqua et al., 2014; Laycock et al., 2007).

130   Single cell studies by Wiesel and Hubel (1966) in lateral geniculate nucleus provided

131   evidence that presenting stimuli on a red background suppresses spiking activity in a class (Type

132   IV) of magnocells (despite the general colour insensitivity of the magnocellular class). These

133   cells have been reported in a number of locations along the magnocellular pathway, including the

134   retinal ganglion cells (de Monasterio, 1978), lateral geniculate nucleus (Wiesel & Hubel, 1966)

135   and striate cortex (Livingstone & Hubel, 1984).

136   Several studies in human have borrowed from the primate results and have used red

137   surrounds to investigate the effects of suppressing magnocellular firing on human perception and

138   action, and have inferred a similar effect in humans based on behavioural performance change in

139   response to red light, typically a weakened or reduced response in healthy controls (Awasthi et al.,

140   2016; Breitmeyer & Breier, 1994; West et al., 2010; but see Hugrass et al., 2018). West et al. (2010)

141   found a temporal precedence effect for fearful faces that are presented on a green background, but

142   this effect is diminished when the stimuli are presented on a red background of the same luminance.

143   The authors interpreted this finding in terms of suppression of magnocellular input - superior

144   colliculus - pulvinar route to the amygdala. However, it is unlikely that a red surround would

145   disrupt early processing via this route, because unlike Type III magnocellular neurons, Type IV

146   magnocellular neurons do not project to the superior colliculus (de Monasterio, 1978), but project

147   solely to the LGN.

148   Interestingly, recent studies have shown that red surrounds have different effects on visual

149   processing for groups with atypical magnocellular processing, such as schizophrenia and high trait

150   schizotypy (Bedwell et al., 2013; Bedwell et al., 2006, 2018; Bedwell & Orem, 2008) dyslexia

151   (Chase et al., 2003; Edwards et al., 1996). For example, Bedwell et al. (2013) examined the effects

152   of a red background on P100 responses to a high contrast check pattern. For people with low trait

153   schizotypy, a red background produced the expected reduction in P100 amplitude, whereas for

5

154   people with high schizotypy, P100 amplitudes did not differ with red and green backgrounds.
155   Similarities in magnocellular functioning in individuals with ASD and schizophrenia (Butler et al.,
156   2005; Kim et al., 2006; Laycock et al., 2007), and the findings that individuals with high AQ and
157   high SPQ scores share a common social factor (Dinsdale et al., 2013; Ford & Crewther, 2014),
158   implies that groups with high versus low AQ groups are likely to show differential processing of
159   stimuli with red versus green backgrounds.

160   Based on West et al.'s (2010) results, it was predicted that low AQ participants would be
161   less accurate in discriminating between fearful and neutral expressions when LSF face stimuli are
162   presented on a red background, than when presented on a green background. Based on the existing
163   literature (Awasthi et al., 2016; West et al., 2010), it was expected that red background would
164   reduce the effects of LSF fearful expression on P100 and N170 amplitudes in the low AQ group.
165   Finally, combining the evidence that both AQ and schizotypy are associated with magnocellular
166   pathway abnormalities (reviewed Laycock et al., 2007), that the AQ and SPQ scales share a
167   common factor (Dinsdale et al., 2013; Ford & Crewther, 2014) and that red backgrounds have
168   different effects on visual processing for groups with low and high schizotypy (Bedwell et al.,
169   2013), it was anticipated that a red background would not influence the amplitude of early EEG
170   responses to fearful faces in the high AQ group.

171   **2. Materials and methods**

172   **2.1. Participants**

173   Participants were recruited within the university and local community through distributed
174   advertisements and word-of-mouth. The inclusion criteria required participants to be aged between
175   18 and 40, have normal (or corrected-to-normal) vision, and have no history of neurological
176   conditions. Prior to the EEG session, participants completed an online version of the AQ
177   questionnaire (Baron-Cohen et al., 2001). Of the 135 AQ respondents, 46 individuals who scored
178   either low or high on the AQ questionnaire were recruited to participate in the EEG study at
179   Swinburne University of Technology, Melbourne, Australia. After screening the EEG data for
180   excessive noise (>75μV signals on a high proportion of trials), 43 participants (25 females) were
181   included in the final sample (age range: 18-31 years, $M = 23.8$; $SD = 4.18$). The Swinburne
182   University Human Research Ethics Committee approved the experimental procedures, and all
183   participants provided written, informed consent prior to participation in accordance with the
184   Declaration of Helsinki.

185   **2.2. Autism-Spectrum Quotient**

186   The AQ (Baron-Cohen et al., 2001) is a self-report questionnaire measuring the degree to which an

187   adult in the general population with normal intelligence has the traits associated with ASD. The 50-

188   item instrument evaluates social skills, attention switching, attention to detail, communication, and

189   imagination. Allocation into the low and high AQ groups was based on the population mean ($M =$

190   18.10, SD= 10.81) for AQ scores (Ruzich et al., 2015). The low (n=21; AQ<11) and high (n=22;

191   AQ>22) AQ groups had mean scores of 8.48 (SD=2.69) and 27.71 (SD=6.17), respectively.

192   **2.3. Visual stimuli**

193   Stimuli were created for our 2 (facial emotion) x 2 (spatial frequency) x 2 (background colour)

194   design. The greyscale fearful and neutral face stimuli (see Figure 1) were taken from the 7 different

195   identities (4 female) from the Nimstim Face Set (Tottenham et al., 2009). To create LSF (<2

196   cycles/degree) and HSF (> 6 cycles/degree) faces, all images were filtered with high-pass and low-

197   pass Gaussian filters (Burt et al., 2017). All pictures were fitted within a frame of 500 x 700 pixels,

198   with the external features (hair, neck and ears) removed. To control for low-level contrast

199   differences between the neutral and fearful faces, only closed-mouth faces were used. The LSF and

200   HSF images were then equated for luminance and RMS contrast using a custom Matlab script (The

201   Mathworks, Natick, MA).

202   The tasks were created and displayed using VPixx software (Version 3.20,

203   www.vpixx.com), and presented on a 27 x 48cm LCD monitor (60Hz refresh rate). The luminance

204   of the green background (CIEx = 0.33, CIEy = 0.60) was psychophysically matched to that of the

205   red background (CIEx = 0.33, CIEy =0.60, L = 31.9cd/m^2).

206

207

208   **Figure 1.** Visual stimuli. The task involved the presentation of a scrambled face (1800ms) on a
209   coloured background, followed by a spatially filtered fearful or neutral face (500ms). After the face
210   disappeared, a central fixation cross cued the participant to report the facial emotion. The
211   experiment was separated into four blocks, in which the fearful and neutral face stimuli were a)
212   LSF on a green background, b) HSF on a green background, c) LSF on a red background and d)
213   HSF on a red background.

214

215   **2.4. Equiluminance**

7

216 The red and green backgrounds were matched for luminance using a centrally presented

217 heterochromatic minimum flicker task, coded in VPixx (VPixx Technologies, Montreal, CA). Red

218 luminance was held constant while subjects adjusted the green luminance to minimize the

219 perception of red-green flicker (Fiorentini et al., 1996). The point of equiluminance was obtained by

220 averaging four adjustment trials. In all subjects, the adjusted green luminance values were close to

221 the physical luminance of the red background (*M difference* =0.54 cd/m^2, *SE*=0.01 cd/m^2).

2.5. Test procedure

223 Participants were seated in a quiet dark room, at a viewing distance of 70cm from the screen. All

224 participants started with the flicker photometry task, followed by a short training block of 10 trials

225 prior to the experiment. To prevent fatigue, the experiment was split into four blocks of 120 trials

226 (two blocks each for the red and green background conditions, with LSF and HSF fearful and

227 neutral faces randomised within each block). The order of the blocks was counterbalanced across

228 participants. In total, there were 60 replications for each of the eight experimental conditions (2

229 background colour x 2 spatial frequency x 2 facial emotion). For all trials a scrambled face

230 (1800ms) was presented before the target face and central fixation cross (500ms). After the face

231 disappeared, participants used a RESPONSEPixx button box, connected to DATAPixx hardware

232 (VPixx Technologies, Montreal, CA), to report whether the expression was fearful (right button) or

233 neutral (left button). The fixation-cross remained on the screen until the participant made a

234 response. Instructions to participants emphasised the importance of accurate decisions over speed.

235 Participants were allowed to rest between blocks. The testing session lasted approximately one

236 hour.

2.6. VEP recording and analysis

238 EEG recordings were made from a 64-channel Quickcap using Scan 4.5 acquisition software

239 (Neuroscan, Compumedics) from parietal, temporal and occipital regions (OZ, O1, O2, O3, P3, P4,

240 P5, P6, P7, P8, PO1, PO2, PO3, PO4, PO5, PO6, PO7 and PO8). Fz was used as the ground

241 electrode site and the linked mastoids were used as the reference channel (Vlamings et al., 2009).

242 EOG electrodes were placed vertically at the upper and lower orbital regions of the right eye to

243 monitor ocular artifact. Electrode impedances were kept below 10KΩ.

244   EEG data were processed using Brainstorm software (Tadel et al., 2011). Each subject's

245 data were band-pass filtered from 0.1-30Hz and re-referenced to the average reference. The vertical

246 EOG channels were used to detect and remove eye-blink artifacts from the data using Signal Space

247 Projection. Epochs were extracted from -200 – 400ms relative to stimulus presentation, and

8

248 baseline subtraction was applied (-200 – 0ms). All epochs containing amplitudes larger than 75µV

249 were removed from the analysis. Separate VEP averages were computed for each of the 2 (spatial

250 frequency) by 2 (background colour) by 2 (facial emotion) conditions, for the low and high AQ

251 groups. On average, 57.6 (*SD* = 3.4) out of 60 trials in each condition survived data cleaning

252 processes, with no significant differences in the number of trials retained across conditions (all

253 comparisons *p*>0.32), or across participants in the low versus high AQ groups (all comparisons *p*>

254 0.16).

255   To improve the signal with respect to noise, the mean responses were extracted for a cluster

256 of occipitotemporal electrodes from the right hemisphere (P8, PO8). These electrodes produced the

257 greatest amplitude P100-N170 responses, and the electrode locations are consistent with previous

258 literature showing a right hemisphere advantage for the processing of faces and emotion

259 expressions (Burt et al., 2017; Bruno Rossion, 2014; Vlamings et al., 2009). P100 and N170

260 amplitudes were then extracted using a routine programmed in LabVIEW (National Instruments,

261 USA). P100 amplitude was defined as the maximum amplitude in the time-window from 80 to

262 140ms after stimulus presentation. N170 amplitude was defined as the negative peak amplitude in

263 the time-window from 150 to 210ms after stimulus presentation. The data were screened for

264 outliers. The data were screened for outliers. For the analysis of P100 amplitude, data from one low

265 AQ participant was excluded due to an outlier for the red background LSF neutral condition.

266   The peak amplitude and latency data were analysed using SPSS Statistics software (SPSS,

267 Version 20, IBM) and JMP (Version 10.0). In order to investigate the effects of background (green,

268 red) on the ERP emotional responses (fear, neutral) with respect to AQ scores (low, high), we

269 conducted separate 2 (background) by 2 (emotion) by 2 (AQ) mixed design ANOVAs for LSF and

270 HSF stimuli, with P100 and N170 amplitudes as the dependent variables. Separate analyses were

271 conducted for LSF and HSF stimuli, on the basis that this reasonably separates magnocellular and

272 parvocellular contributions (Pourtois et al., 2005; Vlamings et al., 2009). Bonferroni corrections (α

273 = 0.0125) for multiple comparisons were applied to all follow-up t-tests.

3. Results

3.1. Behavioral results

276 Means and standard errors for emotion identification accuracies are presented in Figure 2. Accuracy

277 was defined as the percentage of trials when fearful and neutral facial expressions were correctly

278 reported. For both AQ groups, mean accuracy was above 90% for all conditions. Response times

279 were not subject to statistical analysis as participants were instructed to decide as accurately as

280 possible, only after the target face had disappeared (in order to minimise movement artifact during

281   EEG recording). Thus, the values obtained would not truly reflect reaction times to the stimuli. Due
282   to corrupted and/or missing key-press files, only data from 20 low AQ and 20 high AQ participants
283   were included in the analyses.
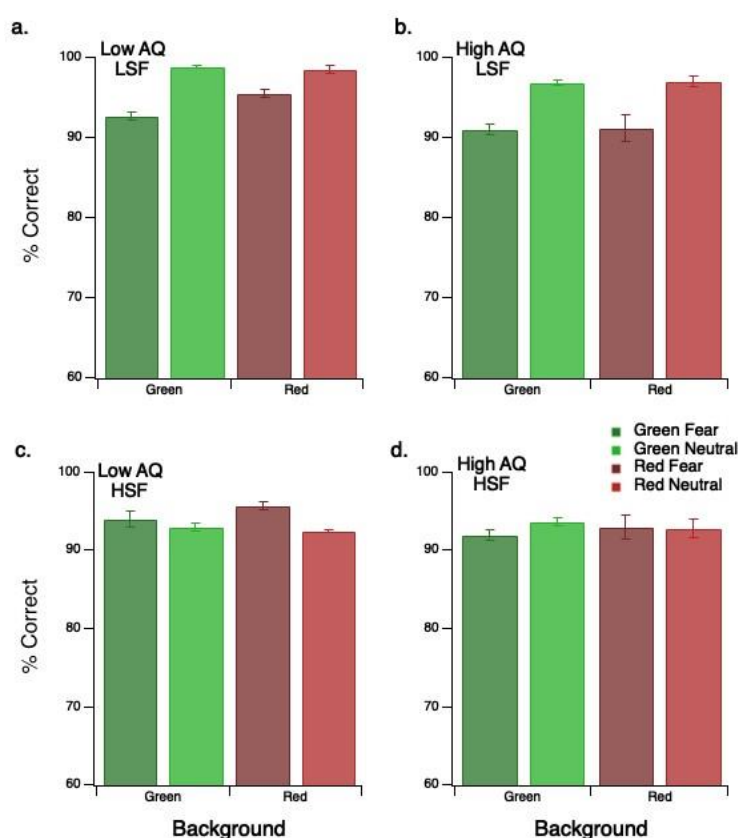
285   **Figure 2.** Mean accuracy levels for emotion identification. Results are presented in separate
286   panels for the low AQ group with (a) LSF and (c) HSF stimuli on green and red backgrounds, and
287   for the high AQ group with (b) LSF and (d) HSF stimuli on green and red backgrounds. Results for
288   the fearful and neutral faces are presented in the darker and lighter bars, respectively. Error bars
289   represent within-subject 1 SEM.

291   For LSF conditions, the three-way (background x emotion x AQ) ANOVA produced a

292   significant main effect of emotion ($F(1,37)=12.45$, $p=0.001$, $\eta_P^2= 0.25$), with greater accuracy for

293   neutral compared to fearful faces. There was also a significant interaction between background,

294   emotion and AQ ($F(1,37)=4.45$, $p=0.041$, $\eta_P^2=0.11$). To explore this interaction, two separate 2

295   (background) x 2 (emotion) ANOVAs were performed for the low and high AQ groups. For the

296   LSF condition, there was a significant background and emotion interaction for the low AQ group

297   ($F(1,19)=10.41$, $p=0.004$, $\eta_P^2=0.35$), with greater accuracy for fearful faces presented on a red

298   background than on a green background. For the high AQ group, there was a significant main effect

299   of emotion ($F(1,18)=6.87$, $p=0.017$, $\eta_P^2=0.28$), with greater accuracy for LSF neutral faces across

300   both background conditions.

10

301   For the HSF conditions, no significant main effects or interactions were evident for either

302   the low or high AQ group.

303   **3.2. VEP results**

304   Grand average ERPs for fearful and neutral, LSF and HSF faces are presented in Figure 3, with

305   separate panels for LSF and HSF conditions for low AQ (Figure 3a and 3c) and for high AQ

306   (Figure 3b and 3d) groups.
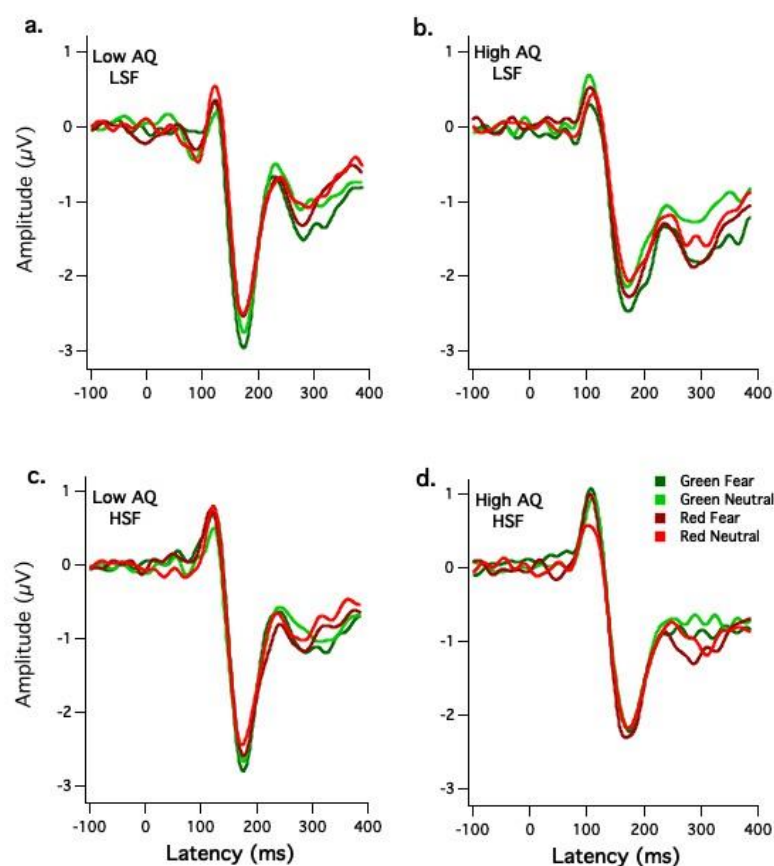
307

308

309   **Figure 3.** Grand averaged cluster waveforms in response to LSF and HSF fearful and neutral
310   faces. The separate panels illustrate responses from the low AQ group for (a) LSF and (c) HSF
311   stimuli, and the high AQ group for (b) LSF and (d) HSF stimuli. For the red background conditions,
312   the dark and light red lines represent fearful and neutral faces, respectively. For the green
313   background conditions, the dark and light green lines represent fearful and neutral faces,
314   respectively.

315

316   **3.2.1. P100 amplitude**

11

317   Figure 4 illustrates the effects of background colour on P100 amplitudes for the low and

318   high AQ groups with LSF (Figures 4a and 4b) and HSF (Figure 4c and 4d) face stimuli. Separate 2

319   (background) x 2 (emotion) x 2 (AQ) ANOVAs were performed for the LSF and HSF conditions.
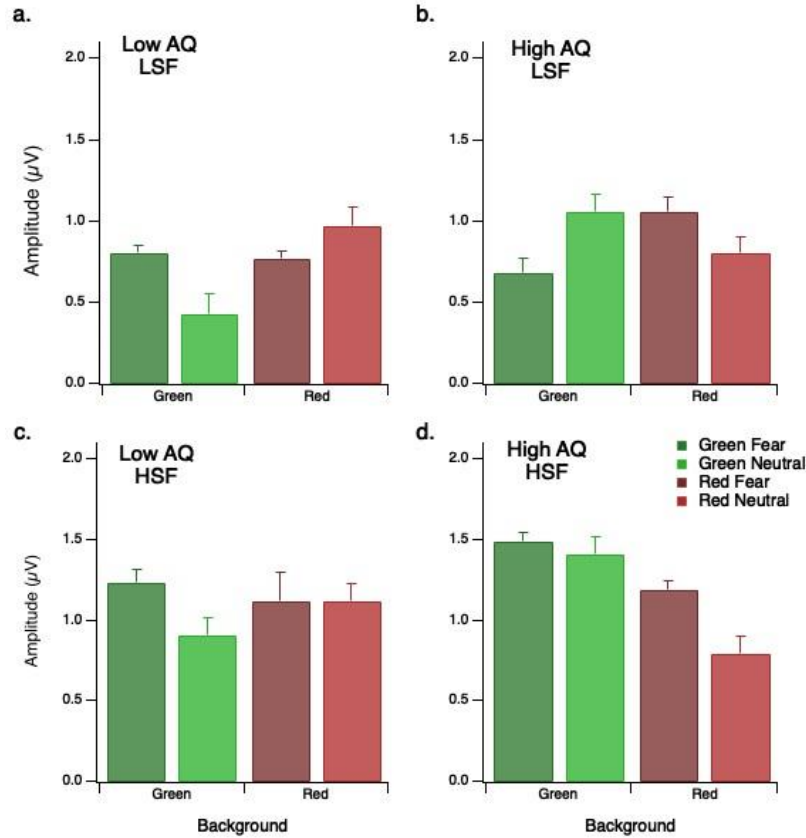
320

Figure 4. Mean P100 amplitudes. Results are presented in separate panels for the low AQ group with (a) LSF and (c) HSF stimuli, and for the high AQ group with (b) LSF and (d) HSF stimuli. Results for the fearful and neutral faces are presented in the darker and lighter bars, respectively. Error bars represent within-subject 1SEM.

326

327   For the LSF condition, there was a significant three-way interaction between the effects of

328   background colour, emotion and AQ $F(1,40)=4.29$, $p=0.045$, $\eta_P^2=0.97$). To investigate this

329   interaction, separate follow-up tests of simple main effects were conducted for the low and high AQ

330   groups (Bonferroni corrected). For the low AQ group, mean P100 amplitudes were higher for LSF

331   fearful faces than LSF neutral faces when the background was green ($\bar{x}_{diff} = 0.24$ μV, $p = 0.024$), but

332   not when the background was red ($\bar{x}_{diff} = 0.02$ μV, $p = 0.703$). For the high AQ group, mean P100

333   amplitudes for LSF fearful and neutral faces differed in the opposite direction, but not significantly,

334   for either the green background ($\bar{x}_{diff} = 0.24$ μV, $p=0.068$) or red background ($\bar{x}_{diff}=0.18$ μV,

335   $p=0.294$) conditions.

336   For the HSF condition, the main effect of emotion was approaching significance

337 ($F(1,41)=3.86$, $p=0.056$), with a tendency for P100 amplitudes to be greater for fearful faces

338 compared to neutral faces. The interaction between background and AQ was also approaching

339 significance ($F(1,41)=3.51$, $p=0.068$). To explore this interaction, follow-up tests of simple main

340 effects were conducted (Bonferroni corrected). On average, P100 amplitudes were higher in

341 response to stimuli presented on a green background than on a red background for the high AQ

342 group ($\overline{x}_{diff} = 0.31$ µV, $p = 0.027$) but not for the low AQ group ($\overline{x}_{diff} = 0.05$ µV, $p = 0.708$).

343 *3.2.1.1. Principle component and factor analysis*

344 To obtain a clearer understanding of the relationships between the stimulus variables as they apply

345 to the hypothetical framework, the P100 amplitudes for LSF fearful and neutral stimuli presented on

346 green and red backgrounds were subjected to a post-hoc principal components analysis (PCA) using

347 maximum likelihood estimation/Varimax rotation. Due to the well-reported relationship of LSF and

348 magnocellular functioning, and the aim of the current study, we conducted this further analysis on

349 LSF stimuli only. Components with Eigenvalues >1.0 were retained as substantial representations

350 of the variation in the model. Component loadings below 0.3 were suppressed in order to report

351 only important component contributions (Tabachnick and Fidell, 2013).

352   Initially, the AQ scores were included in the PCA in order to establish which other variables

353 that the AQ scores related to. The rotated component loading for P100 amplitudes to LSF stimuli

354 plus AQ are presented in Table 1 below. Scores below 0.3 are not shown. The PCA resulted in a

355 three-component solution (explaining 77% variance), with only component 1 being AQ dependent.

356

357 **Table 1.**

358 Rotated component loadings for LSF P100 amplitudes using Maximum Likelihood/Varimax

359 methods

	Component 1	Component 2	Component 3
AQ score	0.500		
Green LSF Fear		0.788	
Green LSF Neutral	0.801		
Red LSF Fear	0.322		0.548
Red LSF Neutral			0.557

360 *Note: Scores below 0.3 are not shown in order to report only important component contributions.*

361

13

362   The individual component scores were calculated and presented as a 3D scatter plot (see

363   Figure 5). Membership of the low AQ and high AQ groups is shown by grey cubes and black

364   spheres respectively. The separation of most of the low AQ data points from the high AQ data

365   points in the 3-factor space clearly shows that autistic tendency plays a role in the strength of the

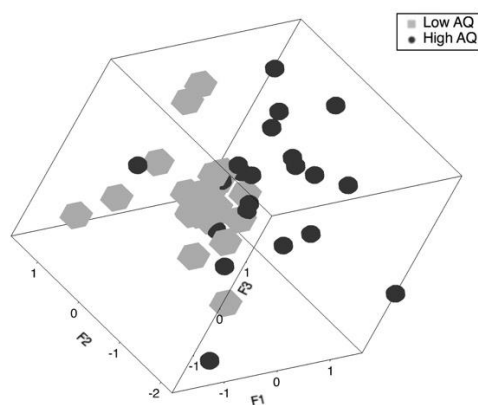366   P100 response for LSF stimuli.

367

368

369   **Figure 5.** 3D component plot of low AQ (grey cube) and high AQ (black sphere) groups plotted as
370   a function of the 3 components. The view chosen shows a clear separation of low and high AQ
371   data points

372

373

374   To further explore factors underlying AQ differences, factor analysis was performed

375   separately for low and high AQ groups, as shown in Table 2 below. Principal components were

376   used as the factoring method with prior communality indexed by squared multiple correlations

377   (SMC), and rotation using Varimax. Only two components reached significance on the Kaiser

378   criterion and hence a two-component solution was developed. For the low AQ group, the first factor

379   coded for fearful faces across red and green backgrounds, while the second factor coded neutral

380   faces across red and green backgrounds (with negative correlations between the amplitudes). In

381   contrast, for the high AQ group, the first factor coded predominately for green backgrounds, with a

382   weaker input from the red neutral variable while the second factor coded for red backgrounds,

383   across all facial emotional expressions.

384

385

14

386 **Table 2.**

387 Separate rotated exploratory factor loadings with Varimax rotation for low and high AQ groups

	Low AQ		High AQ	
	Factor 1	**Factor 2**	**Factor 1**	**Factor 2**
Green LSF Fear	0.483		0.579	
Green LSF Neutral		0.509	0.479	
Red LSF Fear	0.632			0.539
Red LSF Neutral		-0.507	0.408	0.463

388 *Note: Scores below 0.3 are not shown in order to report only important component contributions.*

389   In summary, the analysis demonstrated that the strength of P100 responses for LSF face

390 stimuli is dependent on autistic tendency. It also revealed a different factor structure in which for

391 the low AQ group the factors separated on the basis of emotion while for the high AQ group, they

392 separated more on the basis of background colour.

393

394 **3.2.2. N170 Amplitude**

395   Bar graphs for mean N170 amplitudes, separated by autistic tendency group and spatial

396 frequency are presented in Figure 5. For the LSF condition, the 2 (background) x 2 (emotion) x 2

397 (AQ) ANOVA produced a significant main effect of emotion ($F(1,41)=8.201$, $p=0.007$, $\eta_p^2=0.167$),

398 with greater N170 amplitude for fearful faces compared to neutral faces. There were no other main

399 effects or interactions.

400   For the HSF condition, there were no significant main effects or interactions.
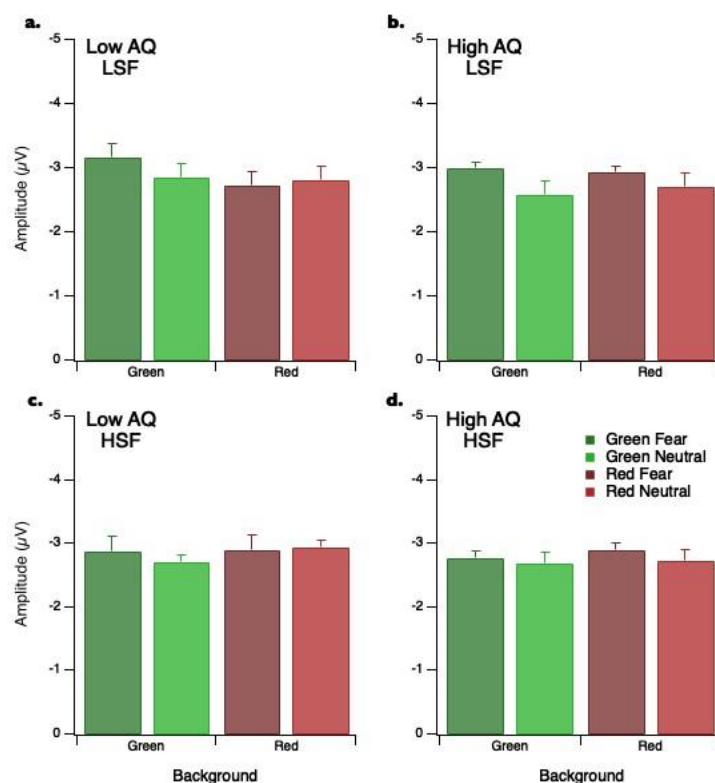
401

402

Figure 6. Mean N170 amplitudes. Results are presented in separate panels for the low AQ group with (a) LSF and (c) HSF stimuli, and for the high AQ group with (b) LSF and (d) HSF stimuli. Results for the fearful and neutral faces are presented in the dark and light grey bars, respectively. Error bars represent within-subject 1SEM.

4. Discussion

This is the first electrophysiological investigation into the effects of a red background on early evoked activity to fearful and neutral facial expressions for groups with low and high autistic tendency. For the LSF face stimuli, there was a complex interaction between the effects of background colour, facial emotion and autistic tendency on P100 amplitudes. This suggests that the effects of a red background on early evoked responses to fearful versus neutral faces may vary for groups with low and high levels of autistic tendency. These effects of background color on responses to facial emotion were not evident for the N170 component. Hence, our discussion focuses on interpreting the P100 responses and providing a theoretical model for explaining the differences in facial emotion processing for groups with low and high AQ scores.

The behavioral data suggest that both the low and high AQ groups were able to accurately identify the facial expressions as neutral or fearful, regardless of the background colour or spatial frequency of the stimuli. For the low AQ group, we found that LSF fearful expressions were identified correctly more often when the faces were presented on a red background than on a green background. This was initially a surprising result in light of West et al.'s (2010) finding that a red

16

425 background extinguishes the temporal precedence for detecting fearful facial expressions. However,

426 given the length of the stimulus exposure duration (500ms), our behavioral results are unlikely to

427 reflect rapid processing mechanisms that are important for temporal order judgements.

428 Previous studies have suggested that the magnocellular pathway allows for rapid

429 transmission of salient information, such as threat, to the amygdala (de Gelder et al., 2011; Méndez-

430 Bértolo et al., 2016; Morris et al., 2001; Vuilleumier et al., 2003). On the basis that magnocellular

431 responses are biased towards LSF input (Benardete & Kaplan, 1999a, 1999b; Kaplan & Shapley,

432 1986), and that type IV magnocellular cells are suppressed by red backgrounds (Wiesel & Hubel,

433 1966), we used both spatial frequency and background colour to probe magnocellular involvement

434 in P100 responses to fearful faces. For the low AQ group, the finding that P100 amplitudes were

435 greater for LSF fearful versus LSF neutral faces on a green background supports evidence of a

436 magnocellular pathway involvement in the rapid processing of threat relevant stimuli. Furthermore,

437 our finding that this difference is extinguished when the faces are presented on a red background

438 indicated that suppressing magnocellular input (specifically Type IV magnocellular input) reduces

439 early processing for threatening versus neutral face stimuli. However, these effects were relatively

440 small, which indicates that using a red background does not greatly influence the variance in P100

441 responses to emotional faces. By contrast, for the high AQ group, there was no significant

442 difference in mean P100 amplitudes for LSF fearful and LSF neutral faces, regardless of whether

443 they were presented on green or red backgrounds. This indicates that for those with high levels of

444 autistic tendency, Type IV magnocellular cells are unlikely to contribute to early processing

445 differences for fearful versus neutral faces.

446 There are similar magnocellular abnormalities in both AQ and schizotypy (reviewed

447 Laycock et al., 2007), and the AQ and SPQ scales share a common factor (Dinsdale et al., 2013;

448 Ford & Crewther, 2014). Our finding that a red background had different effects on P100 responses

449 to LSF faces for groups with low and high AQ appears to parallel those of Bedwell et al. (2013)

450 who found a red background to reduce P100 amplitude for people with low schizotypy, but no

451 change in P100 amplitude to the red background for people with high schizotypy. Findings from the

452 current study and Bedwell et al. imply that a red background may have different effects on

453 individuals with differing magnocellular function, such as those with low and high AQ. However,

454 such comparisons should be considered with caution as the stimuli employed in the current study

455 and Bedwell et al. are not identical. Specifically, considering we presented facial emotional stimuli

456 we can assume that subcortical projections to the amygdala may influence P100 amplitude, whereas

457 Bedwell et al. presented checkerboard stimuli, which are unlikely to drive a strong amygdala

458 response.

17

459   There are also recent reports in primate of wide-field retinal ganglion cells that project
460   directly to the medial sub-division of the inferior pulvinar (Kwan et al., 2019), findings yet to be
461   confirmed in human. For instance, if input to the amygdala is dominated by the LGN-cortical
462   pathways, one might expect a red background to suppress rapid amygdala reactivity to affective
463   stimuli. While there is certainly mixing of information from magnocellular and parvocellular
464   pathways after V1, and there is a strong V1 – pulvinar – extrastriate cortex feed of information
465   (Ahmadlou et al., 2018; Lakatos et al., 2016), such circuitous associations would be arguably less
466   spatial frequency specific and slower (McFadyen et al., 2017), thus less likely to influence P100
467   responses to emotional face stimuli. In comparison, direct pulvinar–hMT connections would be
468   expected to involve rapid processing (Kwan et al., 2019). If input to the amygdala is strongly
469   influenced by these subcortical pathways, one would not expect red backgrounds to reduce rapid
470   amygdala reactivity to fearful facial expressions.

471   Interestingly, however, the PCA/factor analysis performed on the P100 responses for LSF
472   face stimuli showed a factor structure separated on the basis of stimulus emotion for the low AQ
473   group, but on the basis of background color for the high AQ group. This indicates that we cannot
474   exclude the notion that Type IV magnocellular cells are likely to contribute to early processing
475   differences for those with high levels of autistic tendency. Rather, we need to examine how
476   magnocellular inputs to the dorsal cortical stream (the source of the P100 response) might differ
477   anatomically or physiologically as a function of autistic tendency.

478   A potential mechanism to explain general differences in P100 amplitude responses for the
479   low and high AQ group to facial emotional stimuli is an amygdala-driven contrast-gain modulation.
480   Contrast gain effects of amygdala hyper-response to fearful expressions in humans with autism
481   (Amaral et al., 2003), and in animal models of ASD (Markram et al., 2008) are reported to increase
482   hMT and extrastriate early response. Tadayonnejad et al (2016) used effective connectivity analysis
483   of the pulvinar to show that people with generalised social anxiety disorder demonstrated causally
484   increased influential dynamics between pulvinar and higher order visual cortical regions. Similarly,
485   pulvinar manipulation of occipital cortex visual responses is supported by studies on
486   pharmacological agonism and antagonism of pulvinar (Purushothaman et al., 2012) and also the
487   model of amygdala modulation of visual response via pulvinar and thalamic reticular (TRN) (John
488   et al., 2016). Furthermore, such modulation of thalamic gain by amygdala stimulation has received
489   a boost through optogenetic studies in mice (Aizenberg et al., 2019), where optogenetic activation
490   of amygdala amplified tone evoked responses in auditory cortex.

18

491   Thus, a model consistent with red backgrounds producing different effects on P100

492   amplitudes for high versus low AQ individuals can be plausibly constructed via a combination of 1)

493   a hyper responsive amygdala reaction to fear or anxiety generating situations in those with ASD or

494   high AQ (Dalton et al., 2005; Markram et al., 2008); 2) response gain modulation of pulvinar by

495   direct amygdala projections to the TRN; 3) red background suppression of LGN thalamic drive to

496   hMT causing a greater balance of pulvinar-hMT drive and a resultant fear driven emotional

497   attention. Therefore, the differential effects seen with high versus low AQ groups may be

498   explainable through a different weighting of thalamic inputs to parietal cortex through pulvinar and

499   LGN, or from a differential degree of amygdala driven contrast gain modulation, exerted at the

500   pulvinar, for those with high versus low AQ scores.

501   The literature focuses on the idea that the suppressive effects of red backgrounds are only

502   related to magnocellular functioning (Awasthi et al., 2016; Breitmeyer & Breier, 1994; West et al.,

503   2010; Wiesel & Hubel, 1966), while not considering if there are effects on the spatially and

504   chromatically sensitive parvocellular system. To this point, we found that a red background

505   produced a reduction in P100 amplitudes with HSF stimuli for the high AQ group. This finding is

506   reminiscent of the results of Hugrass et al. (2018), who examined the effects of red background on

507   magnocellular and parvocellular non-linear VEP signatures and found red background to suppress

508   parvocellular generated temporal nonlinearity VEPs, and not did influence magnocellular generated

509   VEP signatures. Considering the parvocellular pathway is highly sensitive to (red/green) color,

510   Hugrass et al. suggested that red backgrounds may increase temporal sensitivity in the parvocellular

511   pathway, with an immediate prediction of enhanced L-M color fusion frequencies. Taken together,

512   one should be cautious when utilising red backgrounds to study magnocellular functioning as they

513   may affect parvocellular functioning too.

514   In conclusion, we compared ERPs in response to fearful and neutral faces for groups with

515   low and high levels of autistic tendency. We used red and green backgrounds and LSF and HSF

516   stimuli in order to probe the role of magnocellular visual input in driving early cortical responses to

517   fearful stimuli. For the low AQ group, P100 amplitudes were higher for the LSF fearful than neutral

518   face when the stimuli were presented on a green background, but not when the faces were presented

519   on a red background. However, for the high AQ group, P100 amplitudes were higher for HSF

520   fearful than neutral faces when presented on a green background, but not when faces were

521   presented on a red background. Our findings suggest that presenting face stimuli on a red

522   background alters both magnocellular and parvocellular contributions to the P100 waveform, and

523   that these effects vary for groups with low and high levels of autistic tendency

524   **5. Author contribution statement**

525   EM created the experimental design, performed testing and data collection, and drafted the

526   manuscript. EM and LH analysed the data. LH and DC contributed to manuscript editing. All

527   authors contributed equally to interpreting the results.

528   **6. Conflict of interest statement**

529   The authors declare that research was conducted in the absence of any commercial or financial

530   relationships that could be construed as a potential conflict of interest.

531   **7. References**

532   Adolphs, R., Sears, L., & Piven, J. (2001). Abnormal Processing of Social Information from Faces

533   in Autism. *Journal of Cognitive Neuroscience*, *13*(2), 232–240.

534   https://doi.org/10.1162/089892901564289

535   Ahmadlou, M., Zweifel, L. S., & Heimel, J. A. (2018). Functional modulation of primary visual

536   cortex by the superior colliculus in the mouse. *Nature Communications*, *9*(1), 1–13.

537   https://doi.org/10.1038/s41467-018-06389-6

538   Aizenberg, M., Rolón-Martínez, S., Pham, T., Rao, W., Haas, J. S., & Geffen, M. N. (2019).

539   Projection from the Amygdala to the Thalamic Reticular Nucleus Amplifies Cortical Sound

540   Responses. *Cell Reports*, *28*(3), 605-615.e4. https://doi.org/10.1016/j.celrep.2019.06.050

541   Amaral, D. G., Bauman, M. D., & Mills Schumann, C. (2003). The amygdala and autism:

542   Implications from non-human primate studies: Amygdala and autism. *Genes, Brain and*

543   *Behavior*, *2*(5), 295–302. https://doi.org/10.1034/j.1601-183X.2003.00043.x

544   Awasthi, B., Williams, M. A., & Friedman, J. (2016). Examining the role of red background in

545   magnocellular contribution to face perception. *PeerJ*, *4*, e1617.

546   https://doi.org/10.7717/peerj.1617

547   Baron-Cohen, S., Ring, H. A., Bullmore, E. T., Wheelwright, S., Ashwin, C., & Williams, S. C. R.

548   (2000). The amygdala theory of autism. *Neuroscience & Biobehavioral Reviews*, *24*(3),

549   355–364. https://doi.org/10.1016/S0149-7634(00)00011-7

550 Baron-Cohen, S., Wheelwright, S., Skinner, R., Martin, J., & Clubley, E. (2001). The Autism-

551   Spectrum Quotient (AQ): Evidence from Asperger Syndrome/High-Functioning Autism,

552   Malesand Females, Scientists and Mathematicians. *Journal of Autism and Developmental*

553   *Disorders*, *31*, 5–17.

554 Batty, M., & Taylor, M. J. (2003). Early processing of the six basic facial emotional expressions.

555   *Cognitive Brain Research*, *17*(3), 613–620. https://doi.org/10.1016/S0926-6410(03)00174-5

556 Bedwell, J. S., Chan, C. C., Cohen, O., Karbi, Y., Shamir, E., & Rassovsky, Y. (2013). The

557   magnocellular visual pathway and facial emotion misattribution errors in schizophrenia.

558   *Progress in Neuro-Psychopharmacology and Biological Psychiatry*, *44*, 88–93.

559   https://doi.org/10.1016/j.pnpbp.2013.01.015

560 Bedwell, J. S., Chan, C. C., Trachik, B. J., & Rassovsky, Y. (2013). Changes in the visual-evoked

561   P1 potential as a function of schizotypy and background color in healthy young adults.

562   *Journal of Psychiatric Research*, *47*(4), 542–547.

563   https://doi.org/10.1016/j.jpsychires.2012.12.012

564 Bedwell, J. S., Miller, L. S., Brown, J. M., & Yanasak, N. E. (2006). SCHIZOPHRENIA AND

565   RED LIGHT: FMRI EVIDENCE FOR A NOVEL BIOBEHAVIORAL MARKER.

566   *International Journal of Neuroscience*, *116*(8), 881–894.

567   https://doi.org/10.1080/00207450500516529

568 Bedwell, J. S., & Orem, D. M. (2008). The effect of red light on backward masking in individuals

569   with psychometrically defined schizotypy. *Cognitive Neuropsychiatry*, *13*(6), 491–504.

570   https://doi.org/10.1080/13546800802605755

571 Bedwell, J. S., Spencer, C. C., Chan, C. C., Butler, P. D., Sehatpour, P., & Schmidt, J. (2018). The

572   P1 visual-evoked potential, red light, and transdiagnostic psychiatric symptoms. *Brain*

573   *Research*, *1687*, 144–154. https://doi.org/10.1016/j.brainres.2018.03.002

574 Benardete, E. A., & Kaplan, E. (1999a). The dynamics of primate M retinal ganglion cells. *Visual*

575   *Neuroscience*, *16*(2), 355–368. https://doi.org/10.1017/S0952523899162151

576 Benardete, E. A., & Kaplan, E. (1999b). Dynamics of primate P retinal ganglion cells: Responses to

577   chromatic and achromatic stimuli. *The Journal of Physiology*, *519*(3), 775–790.

578   https://doi.org/10.1111/j.1469-7793.1999.0775n.x

579 Bentin, S., Allison, T., Puce, A., Perez, E., & McCarthy, G. (1996). Electrophysiological Studies of

580   Face Perception in Humans. *Journal of Cognitive Neuroscience*, *8*(6), 551–565.

581   https://doi.org/10.1162/jocn.1996.8.6.551

582 Blau, V. C., Maurer, U., Tottenham, N., & McCandliss, B. D. (2007). The face-specific N170

583   component is modulated by emotional facial expression. *Behavioral and Brain Functions*,

584   *3*(1), 7. https://doi.org/10.1186/1744-9081-3-7

585 Breitmeyer, B. G., & Breier, J. I. (1994). Effects of background color on reaction time to stimuli

586   varying in size and contrast: Inferences about human M channels. *Vision Research*, *34*(8),

587   1039–1045. https://doi.org/10.1016/0042-6989(94)90008-6

588 Burt, A., Hugrass, L., Frith-Belvedere, T., & Crewther, D. (2017). Insensitivity to Fearful Emotion

589   for Early ERP Components in High Autistic Tendency Is Associated with Lower

590   Magnocellular Efficiency. *Frontiers in Human Neuroscience*, *11*, 495.

591   https://doi.org/10.3389/fnhum.2017.00495

592 Butler, P. D., Zemon, V., Schechter, I., Saperstein, A. M., Hoptman, M. J., Lim, K. O., Revheim,

593   N., Silipo, G., & Javitt, D. C. (2005). Early-Stage Visual Processing and Cortical

594   Amplification Deficits in Schizophrenia. *Archives of General Psychiatry*, *62*(5), 495.

595   https://doi.org/10.1001/archpsyc.62.5.495

596 Carr, J. A. (2015). I'll take the low road: The evolutionary underpinnings of visually triggered fear.

597   *Frontiers in Neuroscience*, *9*. https://doi.org/10.3389/fnins.2015.00414

598 Chase, C., Ashourzadeh, A., Kelly, C., Monfette, S., & Kinsey, K. (2003). Can the magnocellular

599   pathway read? Evidence from studies of color. *Vision Research*, *43*(10), 1211–1222.

600   https://doi.org/10.1016/S0042-6989(03)00085-3

601 Corbett, B. A., Carmean, V., Ravizza, S., Wendelken, C., Henry, M. L., Carter, C., & Rivera, S. M.

602   (2009). A functional and structural study of emotion and face processing in children with

603   autism. *Psychiatry Research: Neuroimaging*, *173*(3), 196–205.

604   https://doi.org/10.1016/j.pscychresns.2008.08.005

605 Corradi-Dell'Acqua, C., Schwartz, S., Meaux, E., Hubert, B., Vuilleumier, P., & Deruelle, C.

606   (2014). Neural responses to emotional expression information in high- and low-spatial

607   frequency in autism: Evidence for a cortical dysfunction. *Frontiers in Human Neuroscience*,

608   *8*. https://doi.org/10.3389/fnhum.2014.00189

609 Dalton, K. M., Nacewicz, B. M., Johnstone, T., Schaefer, H. S., Gernsbacher, M. A., Goldsmith, H.

610   H., Alexander, A. L., & Davidson, R. J. (2005). Gaze fixation and the neural circuitry of

611   face processing in autism. *Nature Neuroscience*, *8*(4), 519–526.

612   https://doi.org/10.1038/nn1421

613 de Gelder, B., van Honk, J., & Tamietto, M. (2011). Emotion in the brain: Of low roads, high roads

614   and roads less travelled. *Nature Reviews Neuroscience*, *12*(7), 425–425.

615   https://doi.org/10.1038/nrn2920-c1

616 de Monasterio, F. M. (1978). Properties of concentrically organized X and Y ganglion cells of

617   macaque retina. *Journal of Neurophysiology*, *41*(6), 1394–1417.

618   https://doi.org/10.1152/jn.1978.41.6.1394

619 Derrington, A. M., & Lennie, P. (1984). Spatial and temporal contrast sensitivities of neurones in

620   lateral geniculate nucleus of macaque. *The Journal of Physiology*, *357*(1), 219–240.

621   https://doi.org/10.1113/jphysiol.1984.sp015498

622 Dinsdale, N. L., Hurd, P. L., Wakabayashi, A., Elliot, M., & Crespi, B. J. (2013). How Are Autism

623   and Schizotypy Related? Evidence from a Non-Clinical Population. *PLoS ONE*, *8*(5).

624   https://doi.org/10.1371/journal.pone.0063316

625   Dumas, T., Dubal, S., Attal, Y., Chupin, M., Jouvent, R., Morel, S., & George, N. (2013). MEG

626   Evidence for Dynamic Amygdala Modulations by Gaze and Facial Emotions. *PLoS ONE*,

627   *8*(9), e74145. https://doi.org/10.1371/journal.pone.0074145

628   Edwards, V. T., Hogben, John H, Clark, Craig D, & Pratt, Chris. (1996). *Effects of a Red*

629   *Background on MagnocelluLlar Functioning in Average and Specifically Disabled Readers*.

630   *36*, 9.

631   Eimer, M., & Holmes, A. (2002). An ERP study on the time course of emotional face processing:

632   *Neuroreport*, *13*(4), 427–431. https://doi.org/10.1097/00001756-200203250-00013

633   Fiorentini, A., Porciatti, V., Morrone, M. C., & Burr, D. C. (1996). Visual Ageing: Unspecific

634   Decline of the Responses to Luminance and Colour. *Vision Research*, *36*(21), 3557–3566.

635   https://doi.org/10.1016/0042-6989(96)00032-6

636   Ford, T. C., & Crewther, D. P. (2014). Factor Analysis Demonstrates a Common Schizoidal

637   Phenotype within Autistic and Schizotypal Tendency: Implications for Neuroscientific

638   Studies. *Frontiers in Psychiatry*, *5*. https://doi.org/10.3389/fpsyt.2014.00117

639   Garvert, M. M., Friston, K. J., Dolan, R. J., & Garrido, M. I. (2014). Subcortical amygdala

640   pathways enable rapid face processing. *NeuroImage*, *102*, 309–316.

641   https://doi.org/10.1016/j.neuroimage.2014.07.047

642   Henson, R. N., Goshen-Gottstein, Y., Ganel, T., Otten, L. J., Quayle, A., & Rugg, M. D. (2003).

643   Electrophysiological and Haemodynamic Correlates of Face Perception, Recognition and

644   Priming. *Cerebral Cortex*, *13*(7), 793–805. https://doi.org/10.1093/cercor/13.7.793

645   Hillyard, S. A., & Anllo-Vento, L. (1998). Event-related brain potentials in the study of visual

646   selective attention. *Proceedings of the National Academy of Sciences*, *95*(3), 781–787.

647   https://doi.org/10.1073/pnas.95.3.781

648   Holmes, A., Winston, J. S., & Eimer, M. (2005). The role of spatial frequency information for ERP

649   components sensitive to faces and emotional facial expression. *Cognitive Brain Research*,

650   *25*(2), 508–520. https://doi.org/10.1016/j.cogbrainres.2005.08.003

John, Y. J., Zikopoulos, B., Bullock, D., & Barbas, H. (2016). The Emotional Gatekeeper: A Computational Model of Attentional Selection and Suppression through the Pathway from the Amygdala to the Inhibitory Thalamic Reticular Nucleus. *PLOS Computational Biology*, *12*(2), e1004722. https://doi.org/10.1371/journal.pcbi.1004722

Johnson, M. H. (2005). Subcortical face processing. *Nature Reviews Neuroscience*, *6*(10), 766–774. https://doi.org/10.1038/nrn1766

Kaplan, E., & Shapley, R. M. (1986). The primate retina contains two types of ganglion cells, with high and low contrast sensitivity. *Proceedings of the National Academy of Sciences*, *83*(8), 2755–2757. https://doi.org/10.1073/pnas.83.8.2755

Kim, D., Wylie, G., Pasternak, R., Butler, P. D., & Javitt, D. C. (2006). Magnocellular contributions to impaired motion processing in schizophrenia. *Schizophrenia Research*, *82*(1), 1–8. https://doi.org/10.1016/j.schres.2005.10.008

Krolak-Salmon, P., Vighetto, A., Bertrand, O., & Mauguiere, F. (2004). Early Amygdala Reaction to Fear Spreading in Occipital, Temporal, and Frontal Cortex: A Depth Electrode ERP Study in Human. *Neuron*, *42*, 665–676.

Kveraga, K., Boshyan, J., & Bar, M. (2007). Magnocellular Projections as the Trigger of Top-Down Facilitation in Recognition. *Journal of Neuroscience*, *27*(48), 13232–13240. https://doi.org/10.1523/JNEUROSCI.3481-07.2007

Kwan, W. C., Mundinano, I.-C., de Souza, M. J., Lee, S. C. S., Martin, P. R., Grünert, U., & Bourne, J. A. (2019). Unravelling the subcortical and retinal circuitry of the primate inferior pulvinar. *Journal of Comparative Neurology*, *527*(3), 558–576. https://doi.org/10.1002/cne.24387

Lakatos, P., O'Connell, M. N., & Barczak, A. (2016). Pondering the Pulvinar. *Neuron*, *89*(1), 5–7. https://doi.org/10.1016/j.neuron.2015.12.022

675   Laycock, R., Crewther, S. G., & Crewther, D. P. (2007). A role for the 'magnocellular advantage'

676   in visual impairments in neurodevelopmental and psychiatric disorders. *Neuroscience &*

677   *Biobehavioral Reviews*, *31*(3), 363–376. https://doi.org/10.1016/j.neubiorev.2006.10.003

678   LeDoux, J. E. *The Emotional Brain* (Simon & Schuster, New York, 1996).

679   LeDoux, J. (2003). The Emotional Brain, Fear, and the Amygdala. *Cellular and Molecular*

680   *Neurobiology*, 12.

681   Livingstone, M., & Hubel, D. (1984). Anatomy and physiology of a color system in the primate

682   visual cortex. *The Journal of Neuroscience*, *4*, 309–356.

683   Mangun, G. R. (1995). Neural mechanisms of visual selective attention. *Psychophysiology*, *32*(1),

684   4–18. https://doi.org/10.1111/j.1469-8986.1995.tb03400.x

685   Markram, K., Rinaldi, T., Mendola, D. L., Sandi, C., & Markram, H. (2008). Abnormal Fear

686   Conditioning and Amygdala Processing in an Animal Model of Autism.

687   *Neuropsychopharmacology*, *33*(4), 901–912. https://doi.org/10.1038/sj.npp.1301453

688   McCleery, J. P., Allman, E., Carver, L. J., & Dobkins, K. R. (2007). Abnormal Magnocellular

689   Pathway Visual Processing in Infants at Risk for Autism. *Biological Psychiatry*, *62*(9),

690   1007–1014. https://doi.org/10.1016/j.biopsych.2007.02.009

691   McFadyen, J., Mermillod, M., Mattingley, J. B., Halász, V., & Garrido, M. I. (2017). A Rapid

692   Subcortical Amygdala Route for Faces Irrespective of Spatial Frequency and Emotion. *The*

693   *Journal of Neuroscience*, *37*(14), 3864–3874. https://doi.org/10.1523/JNEUROSCI.3525-

694   16.2017

695   Méndez-Bértolo, C., Moratti, S., Toledano, R., Lopez-Sosa, F., Martínez-Alvarez, R., Mah, Y. H.,

696   Vuilleumier, P., Gil-Nagel, A., & Strange, B. A. (2016). A fast pathway for fear in human

697   amygdala. *Nature Neuroscience*, *19*(8), 1041–1049. https://doi.org/10.1038/nn.4324

698   Morris, J. S., DeGelder, B., Weiskrantz, L., & Dolan, R. J. (2001). Differential extrageniculostriate

699   and amygdala responses to presentation of emotional faces in a cortically blind field. *Brain*,

700   *124*(6), 1241–1252. https://doi.org/10.1093/brain/124.6.1241

Morris, J. S., Friston, K. J., Buchel, C., Young, A. W., Calder, A. J., & Dolan, R. J. (1998). A neuromodulatory role for the human amygdala in processing emotional facial expressions. *Brain*, *121*(1), 47–57. https://doi.org/10.1093/brain/121.1.47

Morris, J. S., Ohman, A., & Dolan, R. J. (1999). A subcortical pathway to the right amygdala mediating "unseen" fear. *Proceedings of the National Academy of Sciences*, *96*(4), 1680–1685. https://doi.org/10.1073/pnas.96.4.1680

Mundinano, IC., Kwan, W. C., & Bourne, J. A. (2019). Retinotopic specializations of cortical and thalamic inputs to area MT. *PNAS, 116,* 23326-23331.

Nakashima, T., Goto, Y., Abe, T., Kaneko, K., Saito, T., Makinouchi, A., & Tobimatsu, S. (2008). Electrophysiological evidence for sequential discrimination of positive and negative facial expressions. *Clinical Neurophysiology*, *119*(8), 1803–1811. https://doi.org/10.1016/j.clinph.2008.04.014

Nassi, J. J., & Callaway, E. M. (2009). Parallel processing strategies of the primate visual system. *Nature Reviews Neuroscience*, *10*(5), 360–372. https://doi.org/10.1038/nrn2619

Nummenmaa, L., Engell, A. D., von dem Hagen, E., Henson, R. N. A., & Calder, A. J. (2012). Autism spectrum traits predict the neural response to eye gaze in typical individuals. *NeuroImage*, *59*(4), 3356–3363. https://doi.org/10.1016/j.neuroimage.2011.10.075

Öhman, A. (2005). The role of the amygdala in human fear: Automatic detection of threat. *Psychoneuroendocrinology*, *30*(10), 953–958. https://doi.org/10.1016/j.psyneuen.2005.03.019

Ohman, A. (2005). The role of the amygdala in human fear: Automatic detection of threat. *Psychoneuroendocrinology*, *30*(10), 953–958. https://doi.org/10.1016/j.psyneuen.2005.03.019

Olivares, E. I., Iglesias, J., Saavedra, C., Trujillo-Barreto, N. J., & Valdés-Sosa, M. (2015). Brain Signals of Face Processing as Revealed by Event-Related Potentials. *Behavioural Neurology*, *2015*, 1–16. https://doi.org/10.1155/2015/514361

727   Pessoa, L. (2010). Emotion and attention effects: Is it all a matter of timing? Not yet. *Frontiers in*

728   *Human Neuroscience*, *4*. https://doi.org/10.3389/fnhum.2010.00172

729   Pessoa, L., & Adolphs, R. (2010). Emotion processing and the amygdala: From a "low road" to

730   "many roads" of evaluating biological significance. *Nature Reviews Neuroscience*, *11*(11),

731   773–782. https://doi.org/10.1038/nrn2920

732   Pourtois, G., Dan, E. S., Grandjean, D., Sander, D., & Vuilleumier, P. (2005). Enhanced extrastriate

733   visual response to bandpass spatial frequency filtered fearful faces: Time course and

734   topographic evoked-potentials mapping. *Human Brain Mapping*, *26*(1), 65–79.

735   https://doi.org/10.1002/hbm.20130

736   Pourtois, G., Grandjean, D., Sander, D., & Vuilleumier, P. (2004). Electrophysiological Correlates

737   of Rapid Spatial Orienting Towards Fearful Faces. *Cerebral Cortex*, *14*(6), 619–633.

738   https://doi.org/10.1093/cercor/bhh023

739   Purushothaman, G., Marion, R., Li, K., & Casagrande, V. A. (2012). Gating and control of primary

740   visual cortex by pulvinar. *Nature Neuroscience*, *15*(6), 905–912.

741   https://doi.org/10.1038/nn.3106

742   Rossion, B. (2003). A network of occipito-temporal face-sensitive areas besides the right middle

743   fusiform gyrus is necessary for normal face processing. *Brain*, *126*(11), 2381–2395.

744   https://doi.org/10.1093/brain/awg241

745   Rossion, Bruno. (2014). Understanding face perception by means of human electrophysiology.

746   *Trends in Cognitive Sciences*, *18*(6), 310–318. https://doi.org/10.1016/j.tics.2014.02.013

747   Ruzich, E., Allison, C., Smith, P., Watson, P., Auyeung, B., Ring, H., & Baron-Cohen, S. (2015).

748   Measuring autistic traits in the general population: A systematic review of the Autism-

749   Spectrum Quotient (AQ) in a nonclinical population sample of 6,900 typical adult males and

750   females. *Molecular Autism*, *6*(1), 2. https://doi.org/10.1186/2040-2392-6-2

751   Silverstein, D. N., & Ingvar, M. (2015). A multi-pathway hypothesis for human visual fear

752   signaling. *Frontiers in Systems Neuroscience*, *9*. https://doi.org/10.3389/fnsys.2015.00101

753   Stein, T., Seymour, K., Hebart, M. N., & Sterzer, P. (2014). Rapid Fear Detection Relies on High

754   Spatial Frequencies. *Psychological Science*, *25*(2), 566–574.

755   https://doi.org/10.1177/0956797613512509

756   Tabachnick BG, & Fidell LS. *Using Multivariate Statistics*. 6 ed. Boston: Allyn and Bacon (2013)

757   Mundinano, IC., Kwan, W. C., & Bourne, J. A. (2019). Retinotopic specializations of

758   cortical and thalamic inputs to area MT. *PNAS, 116,* 23326-23331.

759   Tadayonnejad, R., Klumpp, H., Ajilore, O., Leow, A., & Phan, K. L. (2016). Aberrant pulvinar

760   effective connectivity in generalized social anxiety disorder. *Medicine*, *95*(45).

761   https://doi.org/10.1097/MD.0000000000005358

762   Tadel, F., Baillet, S., Mosher, J. C., Pantazis, D., & Leahy, R. M. (2011). Brainstorm: A User-

763   Friendly Application for MEG/EEG Analysis. *Computational Intelligence and*

764   *Neuroscience*, *2011*, 1–13. https://doi.org/10.1155/2011/879716

765   Tamietto, M., Pullens, P., de Gelder, B., Weiskrantz, L., & Goebel, R. (2012). Subcortical

766   Connections to Human Amygdala and Changes following Destruction of the Visual Cortex.

767   *Current Biology*, *22*(15), 1449–1455. https://doi.org/10.1016/j.cub.2012.06.006

768   Tottenham, N., Tanaka, J. W., Leon, A. C., McCarry, T., Nurse, M., Hare, T. A., Marcus, D. J.,

769   Westerlund, A., Casey, B., & Nelson, C. (2009). The NimStim set of facial expressions:

770   Judgments from untrained research participants. *Psychiatry Research*, *168*(3), 242–249.

771   https://doi.org/10.1016/j.psychres.2008.05.006

772   Vlamings, P. H. J. M., Goffaux, V., & Kemner, C. (2009). Is the early modulation of brain activity

773   by fearful facial expressions primarily mediated by coarse low spatial frequency

774   information? *Journal of Vision*, *9*(5), 12–12. https://doi.org/10.1167/9.5.12

775   Vuilleumier, P., Armony, J. L., Driver, J., & Dolan, R. J. (2003). Distinct spatial frequency

776   sensitivities for processing faces and emotional expressions. *Nature Neuroscience*, *6*(6),

777   624–631. https://doi.org/10.1038/nn1057

778   West, G. L., Anderson, A. K., Bedwell, J. S., & Pratt, J. (2010). Red Diffuse Light Suppresses the

779   Accelerated Perception of Fear. *Psychological Science*, *21*(7), 992–999.

780   https://doi.org/10.1177/0956797610371966

781   Wiesel, T. N., & Hubel, D. H. (1966). Spatial and chromatic interactions in the lateral geniculate

782   body of the rhesus monkey. *Journal of Neurophysiology*, *29*, 1115–1156.

783

784

785

786

787

788

789

790

791

792