Early and late event related potentials are modulated by infant and adult faces of high and low attractiveness

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1   **Abstract**

2   The processing of infant faces may be somewhat distinct from that of adult

3   faces. Indeed, recent neuroimaging studies have provided evidence of an

4   early, "baby-specific" neural response whereby infant faces are perceived

5   more rapidly than adult faces. Using event-related potentials, the present

6   study aimed to determine whether the preferential response to infant faces is

7   present at both early and late stages of face processing, and to investigate

8   the effects of aesthetic appearance on the processing of adult and infant

9   faces by directly manipulating the perceived attractiveness or cuteness within

10   a given face identity. Here, we find evidence for enhanced processing of

11   infant faces, relative to adult faces, at both early (N170, P2) and late (LPC)

12   stages of face processing. We also find that the aesthetic appearance of both

13   infant and adult faces modulates early neural responses, with enhanced

14   responses to less attractive/cute faces as compared to more attractive/cute

15   faces. Overall, our results provide additional evidence for a preferential

16   response to infant faces at early stages of processing, and provide new

17   evidence that this preferential response occurs at later stages of face

18   processing as well, independent of the aesthetic quality of the face or

19   observer sex.

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25   **Keywords**: face processing, attractiveness, baby, N170, LPC

26   **Introduction**

27   Given the importance of parental care for the survival of human infants, and

28   the fact that infant facial morphology differs from that of adults (Bergersen,

29   1966; Enlow & Hans, 1996), the processing of infant faces may be somewhat

30   distinct from that of adult faces. Indeed, behavioral studies have

31   demonstrated that infant faces are attentionally prioritized above adult faces

32   and other social stimuli (Brosch et al., 2007; Cárdenas et al., 2013; Hodsoll et

33   al., 2010; Proverbio, 2011a; Thompson-Booth et al., 2014a, 2014b) and elicit

34   more positive affective responses (Hildebrandt & Fitzgerald, 1978; Senese et

35   al., 2013), stronger arousal responses (Esposito et al., 2014), and even

36   increase careful behavior and focus (Nittono et al., 2012). Some work even

37   suggests that face-processing limitations, such as the other-race effect, may

38   not affect the processing of infant faces (Proverbio, 2011a; but see Hodsoll et

39   al., 2010).

40

41   Infant-typical features, such as a large/bulbous forehead, large eyes, small

42   chin, and close-set features positioned low on the face are related to

43   perceptions of infant cuteness or attractiveness (Alley, 1981; Glocker et al.,

44   2008; Hildebrandt & Fitzgerald, 1979; Little, 2012; Sternglanz et al., 1977).

45   These infantile features are thought to trigger the *Kindchenschema* (Lorenz,

46   1943), an innate releasing mechanism for caretaking behavior and affective

47   orientation towards infants (e.g., Langlois et al., 1995).

48

49   Supporting neuroimaging studies have provided evidence of a "baby-specific"

50   neural response to infant stimuli (e.g., Caria et al., 2012; Grasso et al., 2009;

51   Kringelbach et al., 2008; Parsons et al., 2014; Proverbio et al., 2010a, 2011b).

52   In particular, event-related potential (ERP) studies have shown that early

53   structural encoding responses are larger for infant faces than adult faces

54   (Grasso et al., 2009; Proverbio et al., 2010a, 2011b). Source localization

55   (Proverbio et al., 2010a) and MEG (Kringelbach et al., 2008) techniques

56   suggest that these differences may, at least partly, originate in the

57   orbitofrontal cortex – a key region implicated in reward processing

58   (Kringelbach & Radcliffe, 2005) and parental behavior (Parsons et al., 2013a).

59   One interpretation of the foregoing results is that baby faces are more

60   rewarding, which may act to facilitate motivation for caretaking responses.

61

62   When viewing adult faces early indices of visual processing, including the

63   N170 ERP component, are modulated by facial attractiveness (Chen et al.,

64   2012; Marzi & Viggiano, 2010; Pizzagalli et al., 2002; Schacht et al., 2008;

65   Werheid et al., 2007; Zhang & Deng, 2012). Facial attractiveness also has

66   effects in later stages of face processing wherein affective and identity

67   information is extracted from faces. For example, the late positive component

68   (LPC), which is thought to reflect heightened processing linked to motivation

69   and attention, is modulated by the attractiveness of adult faces (Chen et al.,

70   2012; Johnston & Oliver-Rodríguez, 1997; Marzi & Viggiano, 2010; Oliver-

71   Rodríguez et al., 1999; Schacht et al., 2008; Werheid et al., 2007; Zhang et

72   al., 2011, 2012).

73

74   While previous research has investigated the time course of attractiveness

75   processing in adult faces, less work has been done exploring the processing

76   of infant facial appearance. The attentional bias for infant faces over adult

77   faces previously observed is positively correlated with subjective arousal

78   ratings of the infant stimuli (Brosch et al., 2007), suggesting that the aesthetic

79   quality of infant faces may influence how efficiently these faces are

80   processed. Furthermore, infant's faces are attentionally prioritized above

81   children's faces (Thompson-Booth et al., 2014b) providing additional support

82   for the notion that cuteness, which is linked to baby-like appearance (Little,

83   2012), may modulate the processing of infant faces. In a study comparing

84   responses to infant and prepubertal-children's faces, Proverbio et al. (2011b)

85   observed an increased N2 response to infant faces compared to older

86   children's faces in women but not men, suggesting that baby schema may

87   modulate the early processing of faces, at least in women. In the same study,

88   however, no differences between infant and children's faces were observed at

89   either P1 or N170 in men or women. While Proverbio et al's (2011b) findings

90   provide equivocal support for the hypothesis that baby schema may modulate

91   face processing, Glocker et al. (2009) demonstrated, in a sample of

92   nulliparous young women, that experimentally manipulating baby schema in

93   infant faces modulated activation in neural regions associated with the

94   processing of rewards (i.e., the nucleus accumbens), providing additional

95   support for this hypothesis. There is also evidence that structural

96   abnormalities that disrupt the baby schema, such as cleft lip and palate, result

97   in processing disruptions (i.e. a diminished "baby-specific" neural response,

98   Parsons et al., 2013b). Together, these studies suggest that the cuteness

99   (i.e., aesthetic quality) of infant faces may modulate the processing of infant

100   faces.

101

102 Both men and women show increased early neural responses to infant faces

103 compared to adult faces (Proverbio et al., 2010a, 2011b). Evidence suggests

104 that women also show an age coding effect in the left hemisphere (i.e. larger

105 responses to infant faces than adult faces) that is not consistently observed in

106 men (Proverbio et al., 2010a, 2011b). Although some behavioral studies also

107 suggest that women respond more strongly to infant faces than men do (e.g.,

108 Cárdenas et al., 2013; Charles et al., 2013; Hahn et al., 2013), others find no

109 evidence of a sex difference (e.g., Brosch et al., 2007; Parsons et al., 2011a).

110 While evidence for a sex difference in responses to infant faces generally may

111 be equivocal, there is more consistent evidence that women show stronger

112 differential responses to infant facial cuteness than men do (Archer & Monton,

113 2011; Hahn et al., 2013; Lobmaier et al., 2010; Sprengelmeyer et al., 2009;

114 Yamamoto et al., 2009; c.f. Sprengelmeyer et al., 2013). As such, differences

115 in the aesthetic quality of stimuli across studies could, at least partly, explain

116 discrepancies in reported sex differences.

117

118 The present study had three main aims: (1) to determine whether the

119 preferential response to infant faces is present at both early and late stages of

120 face processing, (2) to investigate the effects of aesthetic appearance on the

121 processing of adult and infant faces by directly manipulating the perceived

122 attractiveness or cuteness within a given face identity, and (3) to explore

123 possible sex differences in the processing of infant face stimuli. We used an

124 ERP design to investigate the time course of men's and women's responses

125 to infant and adult faces. Given that the LPC reflects attentional/motivational

126 processing and infant faces tend to be attentionally prioritized, we predicted

127 that the preferential response to infant faces previously observed at early

128 indices of visual processing would also be apparent for the LPC. Based on

129 previous work demonstrating that attractiveness modulates both early and late

130 ERPs for adult facial stimuli, we also anticipated that manipulating the

131 cuteness of our infant facial stimuli and attractiveness of our adult facial

132 stimuli would similarly modulate these ERP responses. Finally, given that

133 women tend to respond more strongly to social stimuli generally (e.g.,

134 Proverbio et al., 2008) and that there is some evidence that they are more

135 sensitive to subtle cues of infant cuteness than are men (e.g., Lobmaier et al.,

136 2010), we predicted that if manipulating infant appearance did have a

137 modulatory effect on ERP responses, this effect might be more apparent in

138 women than in men.

139

140 **Methods**

141 *Participants*

142 15 men and 15 women between the ages of 18 and 31 years (mean = 22.1,

143 SD = 2.6) volunteered for the current study. Participants were recruited

144 through the Psychology subject pool at Western Washington University and

145 were compensated with experimental credits. All participants provided

146 informed consent prior to participation. This study was approved by the

147 Institutional Review Board at Western Washington University. Demographic

148 data including age, sexual orientation, parental status, contact with children,

149 and contraceptive use (women only), were collected from all participants.

150 Sexual orientation was assessed on a 7-point Likert scale where 1 =

151   completely homosexual, 4 = bisexual, and 7 = completely heterosexual. Data

152   from one participant who identified as homosexual was excluded from the

153   analyses reported below (we note here, however, that retaining this individual

154   in the dataset did not alter the pattern of results reported below). Additionally,

155   one participant who reported having children was excluded from subsequent

156   analyses (note: nulliparous samples are commonly used when investigating

157   responses to infant cuteness, e.g. Glocker et al., 2009; Hahn et al., 2015a,

158   2015b). All remaining participants reported little to no contact with children

159   (mean weekly contact = 1.0 hours, SD = 1.8). Handedness was assessed

160   using the Edinburgh handedness questionnaire (EHQ; Oldfield, 1971). Two

161   participants (1 male, 1 female) reporting left-hand dominance were excluded

162   from subsequent analyses. The final analyses reported here included 13

163   heterosexual men and 13 heterosexual women, all of whom were right-

164   handed and none of whom had children.

165

166   *Stimuli*

167   Following previous methodology (Hahn et al., 2013), 35 male, 35 female, and

168   35 infant composite faces were created by averaging the shape, color, and

169   texture cues of two individual faces (see Tiddeman et al., 2001 for more

170   information regarding these computer graphic techniques). Attractiveness

171   (adult faces) and cuteness (infant faces) prototypes that had been previously

172   manufactured (see Hahn et al., 2013) were then used to modify the 2D linear

173   shape of the facial composites by applying a transform based on a proportion

174   of the difference in shape between the high-attractive/cute and low-

175   attractive/cute prototypes to each face in order to manipulate the aesthetic

176   appearance within a given identity. Each composite face was transformed -

177   50% in attractiveness/cuteness (based on shape cues alone) to create the

178   low-aesthetic version and +50% attractiveness/cuteness to create the high-

179   aesthetic version (see Figure 1).

180

181   To ensure that the transforms reliably affected perceived

182   attractiveness/cuteness, the stimuli were evaluated by 98 heterosexual raters

183   (27 male, 71 female; mean age = 23.3 years, SD = 6.5) in a 2-alternative

184   forced choice paradigm. Raters saw the high- and low-aesthetic version of

185   each face and were asked to indicate which face they thought was more

186   attractive (adult faces) or cute (infant faces). Male, female, and infant faces

187   were presented in separate blocks. The order in which the stimuli groups and

188   composite faces within each group were presented was randomized across

189   participants. Similarly, the presentation of the high- and low-aesthetic versions

190   of each face on the right or left side of the screen was randomized across

191   trials. Responses on this preference test were recorded as 0 = preference for

192   low-aesthetic version or 1 = preference for high-aesthetic version. Mean

193   preference scores across the set of stimuli ranged from 0.48 to 0.95. Chi-

194   square tests indicated that for all but five of the 105 composite identities, the

195   high-aesthetic version was chosen as more attractive/cute than the low-

196   aesthetic version at levels significantly greater than chance (all $p < .05$). There

197   was no significant preference for the high-aesthetic version of the remaining 5

198   faces (1 infant, 3 female, 1 male; all ps >.10).

199   [INSERT FIGURE 1 ABOUT HERE]

200

201   *EEG apparatus and recording*

202   Stimuli were presented in full color on a 19-inch Dell LCD monitor. Stimulus

203   presentation and response recording were controlled by in-house software

204   written in Visual Basic. All responses were made with a Cedrus 8-button box

205   (Cedrus Corporation, San Pedro, CA, USA). EEG was continuously recorded

206   from 64 scalp sites, using BioSemi ActiveTwo Ag/AgCl electrodes and

207   hardware (Biosemi, Amsterdam, The Netherlands). The electrodes were

208   placed according to the 10-5 electrode system (Oostenveld & Praamstra,

209   2001), using a nylon electrode cap. EEG signals were amplified with a

210   bandpass of DC-104 Hz by BioSemi ActiveTwo amplifiers, sampled at 512

211   Hz.

212

213   *Procedure*

214   During EEG recording, participants were seated in a dimly lit room. They were

215   instructed to fixate on a cross in the center of the screen and minimize eye or

216   body movements during the recording period. EEG data were collected over

217   two sets of two blocks. Within a block, each of the 105 composite identities

218   was presented in either the high-aesthetic or low-aesthetic version. The

219   alternate version of the face was then presented in the subsequent block such

220   that each identity was only displayed once per block. The two sets contained

221   identical blocks, however the selection of high- vs. low-aesthetic faces

222   allocated into the first and second block was randomized between sets (total

223   of 105 trials per block x 2 blocks per set x 2 sets = 420 trials). Each trial

224   began with the presentation of a red fixation cross at the center of a gray

225   background (rgb: 128, 128, 128). A face was then displayed in the center of

226   the screen for 1000ms, after which time a rating task was presented whereby

227   participants were asked to rate the attractiveness (adult faces) or cuteness

228   (infant faces) on a 5-point scale where 1= not at all attractive/cute and 5 =

229   very attractive/cute. Responses were provided using the button box. The trial

230   ended when a response was made. Trials were separated by a random

231   interstimulus interval between 500 and 1000-ms. Participants were allowed a

232   short (1-2 min) break between blocks.

233

234   *EEG data processing and analysis*

235   Off-line segmentation and averaging of EEG signals was performed with

236   EEGlab v6.01b (Delorme & Makeig, 2004), running on Matlab 7.3.0

237   (Mathworks, Inc., Natick, MA, USA). In a small number of cases, a single

238   channel demonstrated excessive noise and was replaced by a new channel

239   derived by spherical interpolation of the surrounding channels. After

240   downsampling from 512 to 256 samples per second, data were bandpassed

241   between .5 and 20 Hz. We used an independent component analysis (ICA)

242   approach to isolate artifacts and noise sources (Jung et al., 2000). First, we

243   performed an ICA decomposition on the continuous data of each participant.

244   We then manually inspected spatial and temporal properties of the

245   components and removed those that clearly captured artifacts such as eye

246   blinks, eye movement and muscle artifacts. Epochs time locked to the onset

247   of the face stimuli were extracted from the cleaned data using a time window

248   of -100ms to 800ms. Trials were automatically classified as containing an

249   artifact if they had a peak voltage that exceeded 100 uV, a peak to peak

250   voltage greater than 100 uV within a 100ms moving window, or a sample to

251   sample change of greater than 30 uV. All trials containing artifacts were

252   rejected from further analysis. An average of 3.46 trials were rejected from the

253   male participants and 11 trials from the female participants. The remaining

254   trials were averaged separately for each condition.

255

256   Four components of the ERP waveforms were analyzed: (1) P1 (90-100ms)

257   for electrodes PO7 and PO8; (2) N170 (120-200ms) for electrodes P7 and P8;

258   (3) P2 (200-250MS) for electrodes PO3 and PO4; (4) Late Positive

259   Component (LPC) (300-700ms in 50ms intervals) for electrodes POz and Pz.

260   We selected channels at which ERP components showed the greatest

261   amplitude. The sites selected for focused analysis were consistent with

262   previous research for each of the four components. For the P1, N170 and P2

263   components, we measured amplitude and latency of the peak response.

264   Following Werheid et al. (2007), the mean amplitude of the LPC was

265   measured within eight consecutive time periods of equal duration from 300ms

266   to 700ms: (300-350ms, 350-400ms, 400-450ms, 450-500ms, 500-550ms,

267   550-600ms, 600-650ms, 650-700ms). ERP data for the P1, N170, and P2

268   components were subjected to multifactorial repeated-measures ANOVAs

269   with *hemisphere* (left, right), *face type* (infant, same-sex, opposite-sex) and

270   *aesthetic* (high-attractiveness/cuteness, low-attractiveness/cuteness) as

271   within-subject factors and *participant sex* (male, female) as a between-subject

272   factor. A similar analysis was conducted for the LPC component, using a

273   model in which hemisphere was not included; instead, data from electrodes

274   POz and Pz were averaged for the analysis. All statistical analyses were

275   performed in SPSS version 20.0.

276

277   **Results**

278   Because there is evidence of an opposite-sex bias in face processing among

279   heterosexual individuals (e.g., Proverbio et al., 2010b), the sex of the adult

280   facial stimuli was coded relative to the participant (i.e., same-sex or opposite-

281   sex) for all analyses reported here.

282

283   *Behavioral Data*

284   For the attractiveness/cuteness ratings, a 3x2x2 mixed design ANOVA was

285   conducted in which *face type* (infant, same-sex, opposite-sex) and *aesthetic*

286   (high, low) were within-subject factors and *participant sex* (male, female) was

287   a between-subject factor. While there was no main effect of *face type*

288   (Greenhouse-Geisser corrected: $F(1.4,33.5) = 2.01$, $MSE = 0.55$, $p = .16$, η^2

289   $= 0.06$) or *participant sex* ($F(1,24) = 0.66$, $MSE = 0.20$, $p = .43$, $\eta^2 = 0.03$),

290   there was a significant interaction between *face type* and *participant sex*

291   (Greenhouse-Geisser corrected: $F(1.4,33.5) = 7.67$, $MSE = 0.55$, $p = .005$, η^2

292   $= 0.23$). Independent samples t-tests, using a Bonferroni corrected alpha of

293   .017, showed that men and women gave similar ratings, on average, to the

294   infant faces ($t(24) = -0.37$, $p = .716$, mean difference $= -0.10$, SE mean

295   difference $= 0.28$) and same-sex faces ($t(24) = -0.85$, $p = .406$, mean

296   difference $= -0.17$, SE mean difference $= 0.20$), but men rated opposite-sex

297   faces significantly higher than women did ($t(24) = 3.91$, $p = .001$, mean

298   difference $= 0.69$, SE mean difference $= 0.18$).

299

300   There was a main effect of *aesthetic* (F (1,24) = 140.62, *MSE* = 0.02, *p* <

301   .001, η^2 = 0.83), such that the high-aesthetic versions (mean = 3.03, SEM =

302   .09) of the faces were rated as more attractive/cute than the low-aesthetic

303   versions (mean = 2.76, SEM = .08). This main effect was qualified by an

304   interaction with *participant sex* (F(1,24) = 4.59, *MSE* = 0.02, *p* = .043, η^2 =

305   0.03). An independent samples t-test on the average difference scores

306   between the high and low aesthetic versions of faces (regardless of face type)

307   showed that men differentiated less than women did (t(24) = -2.14, *p* = .043,

308   mean difference = -0.10, SE mean difference = 0.05).

309

310   The two-way interaction between *aesthetic* and *face type* was also significant

311   (F (2,48) = 10.71, *MSE* = 0.01, *p* < .001, η^2 = 0.29). To explore this interaction

312   further, we calculated difference scores for each *face type* by subtracting the

313   average rating of the low-aesthetic versions from the average ratings of the

314   high-aesthetic versions. Paired t-tests, using a Bonferroni corrected alpha of

315   .017, of these *difference scores* revealed that the degree to which high-

316   aesthetic versions were rated as more attractive/cute than low-aesthetic

317   versions was greater for opposite-sex faces than either infant faces (t(25) =

318   4.13, *p* < .001, $\text{mean}_{\text{opposite-sex difference score}}$ = 0.39, $\text{SD}_{\text{opposite-sex difference score}}$ =

319   0.23, $\text{mean}_{\text{infant difference score}}$ = 0.20, $\text{SD}_{\text{infant difference score}}$ = 0.15) or same-sex

320   faces (t(25) = 3.25, *p* = .003, $\text{mean}_{\text{same-sex difference score}}$ = 0.22, $\text{SD}_{\text{same-sex difference}}$

321    $_{\text{score}}$ = 0.16). There was no difference in the aesthetic effect for ratings of

322   infant faces compared to same-sex faces (t(25) = -0.59, *p* = .56).

323

324   The three-way interaction between *aesthetic, face type* and *participant sex*

325   approached significance ($F(2,48) = 2.67$, $p = .080$, $\eta^2 = 0.07$) and was driven

326   by the fact that the aesthetic manipulation had a similar effect on women's

327   and men's ratings for the cuteness of infant faces ($t(24) = 1.18$, $p = .25$, mean

328   difference = 0.07, SE mean difference = 0.06) and the attractiveness of same

329   sex adult faces ($t(24) = 0.19$, $p = .85$, mean difference = 0.01, SE mean

330   difference = 0.06), while the aesthetic manipulation had a larger effect on

331   women's ratings of the attractiveness of opposite-sex adult faces it did for

332   men ($t(24) = 2.60$, $p = .016$, Bonferroni corrected alpha = .017, mean

333   difference = 0.21, SE mean difference = 0.08, see Figure 2).

334

335   [INSERT FIGURE 2 ABOUT HERE]

336   *P1 Amplitude*

337   We observed a three-way interaction between *hemisphere, face type,* and

338   *participant sex* ($F(2,48) = 3.73$, $MSE = 1.53$, $p = .031$, $\eta^2 = 0.13$) for P1

339   amplitudes. We further explored this interaction by calculating the magnitude

340   of the right-hemisphere bias (i.e. peak amplitude at PO8 minus peak

341   amplitude at PO7) in response to infant faces, same-sex faces, and opposite-

342   sex faces. Multivariate ANOVA indicated that the magnitude of the sex

343   difference in right-hemisphere bias (i.e. males > females) was largest for

344   opposite-sex adult faces ($F(1,24) = 4.02$, $MSE = 13.28$, $p = .056$, $\eta^2 = 0.14$),

345   followed by same-sex adult faces ($F(1,24) = 3.00$, $MSE = 15.98$, $p = .096$, η^2

346    $= 0.11$), and relatively unapparent for infant faces ($F(1,24) = 0.57$, $MSE =$

347   15.79, $p = .459$, $\eta^2 = 0.02$). There were no other significant effects or

348　　interactions in our main analysis of P1 peak amplitudes (all $F < 3.20$, all $p >$

349　　.086, all $\eta^2 < 0.12$).

350

351　　*P1 Latency*

352　　There were no modulatory effects of *face type, aesthetic,* or *participant sex* for

353　　P1 peak latencies (all $F < 3.47$, all $p > .075$, all $\eta^2 < 0.12$).

354

355　　*N170 Amplitude*

356　　N170 amplitudes were modulated by *face type* ($F(2,48) = 22.53$, $MSE = 2.83$,

357　　$p < .001$, $\eta^2 = 0.47$) and *aesthetic* ($F(1,24) = 6.60$, $MSE = 0.83$, $p = .017$, $\eta^2 =$

358　　0.20). Helmert contrasts indicated that peak N170 amplitudes were larger (i.e.

359　　more negative) for infant faces than adult faces ($F(1,24) = 31.69$, $MSE =$

360　　1.49, $p < .001$, $\eta^2 = 0.57$), while no differences were observed for responses

361　　to same-sex and opposite-sex adult faces ($F(1,24) = 0.83$, $MSE = 0.84$, $p =$

362　　.373, $\eta^2 = 0.03$; see Figure 3). Similarly, peak N170 amplitudes were larger for

363　　the low-aesthetic versions of faces (mean = -4.08, SEM = 0.55) than the high-

364　　aesthetic versions (mean = -3.82, SEM = 0.55). No other effects or

365　　interactions reached significance (all $F < 1.96$, all $p > .17$, all $\eta^2 < 0.07$).

366

367　　　　　　　　　　　　　[INSERT FIGURE 3 ABOUT HERE]

368

369　　*N170 Latency*

370　　There were no effects of *face type, aesthetic,* or *participant sex* for N170 peak

371　　latencies (all Greenhouse-Geisser corrected $F < 2.12$, all $p > .14$, all $\eta^2 <$

372　　0.08).

373

374 *P2 Amplitude*

375 P2 peak amplitude was modulated by *aesthetic* ($F(1,24) = 6.52$, $MSE = 0.99$,

376 $p = .017$, $\eta^2 = 0.19$), with greater peak amplitudes observed for the low-

377 aesthetic versions (mean = 6.11, SEM = 0.61) than the high-aesthetic

378 versions (mean = 5.82, SEM = 0.63) for all face types.

379

380 There was a significant interaction between *face type* and *participant sex* (F

381 $(2,48) = 4.97$, $MSE = 2.83$, $p = .011$, $\eta^2 = 0.16$), and the higher-order

382 interaction between *face type, participant sex*, and *hemisphere* approached

383 significance ($F(2,48) = 3.08$, $MSE = 0.96$, $p = .055$, $\eta^2 = 0.11$). Repeating the

384 analysis separately for men and women revealed that men showed a main

385 effect of *face type* ($F(2,24) = 10.29$, $MSE = 1.58$, $p = .001$, $\eta^2 = 0.46$) but no

386 interaction between *face type* and *hemisphere* ($F(2,24) = 0.38$, $MSE = 1.03$, p

387 $= .69$, $\eta^2 = 0.03$), while women tended to show an interaction between *face*

388 *type* and *hemisphere* (Greenhouse-Geisser corrected: $F(1.27,15.25) = 3.77$,

389 $MSE = 1.40$, $p = .063$, $\eta^2 = 0.24$) but no main effect of *face type* ($F(2,24) =$

390 2.03, $MSE = 4.09$, $p = .62$, $\eta^2 = 0.04$). Helmert contrasts showed that the main

391 effect of *face type* seen in men reflected increased peak P2 amplitudes in

392 response to infant faces were than the other face types (i.e., same-sex and

393 opposite-sex, $F(1,12) = 15.12$, $MSE = 3.02$, $p = .002$, $\eta^2 = 0.56$), while

394 responses to same-sex and opposite-sex faces did not differ ($F(1,12) = 1.76$,

395 $MSE = 2.28$, $p = .21$, $\eta^2 = 0.13$). For women, although there was no main

396 effect of *face type*, the interaction observed between *hemisphere* and *face*

397 *type* indicated that the magnitude of the right and left hemisphere response

398 was similar for infant and opposite-sex faces, but differed for same-sex faces,

399 with an increased response in the left hemisphere (PO3) relative to the right

400 hemisphere (PO4) for this face type. There were no other significant effects or

401 interactions in our main analysis (all F < 3.16, all p > .08, all η^2 < 0.10).

402

403 *P2 Latency*

404 P2 latencies were modulated by *face type* (F (2,48) = 7.55, *MSE* = 93.08, *p* =

405 .001, η^2 = 0.20). Pairwise comparisons, using a Bonferroni corrected alpha of

406 .017, showed that responses to infant faces were significantly delayed

407 compared to opposite-sex faces (*p* = .005, mean difference = 4.96ms, SE

408 mean difference = 1.61) and tended to be delayed compared to same-sex (*p*

409 = .034, mean difference = 3.83ms, SE mean difference = 1.71), no difference

410 in latency was observed between same-sex and opposite-sex adult faces,

411 however (*p* = .280, mean difference = 1.14ms, SE mean difference = 1.03).

412 There was also a main effect of *participant sex* (F (1,24) = 11.48, *MSE* =

413 972.28, *p* = .002, η^2 = 0.32), such that men had delayed P2 latencies (mean =

414 227.34ms, SEM = 2.50) compared to women (mean = 215.38ms, SEM =

415 2.50). The effect of *face type* was qualified by an interaction with *participant*

416 *sex* (F (2,48) = 6.61, *MSE* = 93.08, *p* = .003, η^2 = 0.17). Separate analyses for

417 men and women revealed that this main effect of *face type* was present in

418 men (F (2,24) = 9.31, *MSE* = 138.94, *p* = .001, η^2 = 0.44) but not women (*F*

419 (2,24) = 0.52, *MSE* = 47.23, *p* = .60, η^2 = 0.04).

420

421 The main effect of *hemisphere* (F (1,24) = 6.54, *MSE* = 123.62, *p* = .017, η^2 =

422 0.21) indicated that P2 peak latencies were delayed in the left hemisphere

423   (PO3: mean = 222.97ms, SEM = 2.07) relative to the right hemisphere (PO4:

424   mean = 219.75ms, SEM = 1.66). Finally, *aesthetic* was shown to modulate P2

425   peak latencies (F (1,24) = 6.54, MSE = 64.44, p = .017, η^2 = 0.20), with

426   delayed responses to the low-aesthetic versions of the faces (mean =

427   222.53ms, SEM = 1.87) compared to the high-aesthetic versions (mean =

428   220.20ms, SEM = 1.77). There were no other significant effects or

429   interactions (all F < 2.68, all p > .11, all η^2 < 0.11).

430

431   *LPC*

432   For each of the eight timeframes of the LPC, a 3x2x2 mixed design ANOVA

433   was conducted in which *face type* (infant, same-sex, opposite-sex) and

434   *aesthetic* (high, low) were within-subject factors and *participant sex* (male,

435   female) was a between-subject factor and peak amplitude served as the

436   dependent variable. As seen in Figure 4, there was a consistent, significant

437   effect of *face type* at all LPC windows (all F(2,48) > 4.05, all MSE < 1.91, all p

438   < .024, all η^2 > 0.14) with the exception of 550-600ms and 600-650ms (both F

439   (2,48) < 1.03, both MSE > 1.86, both p > .36, both η^2 < 0.05). At 300-550ms

440   (i.e. the first 5 time windows), Helmert contrasts indicated that LPC peak

441   amplitudes were greater in response to infant faces than either opposite-sex

442   or same-sex adult faces (all p < .03), no significant differences between the

443   face types were observed for 550-650ms (both p > .22), and at the last time

444   window (650-700ms), infant faces elicited the lowest LPC amplitudes (p =

445   .02). Across all time windows, no differences were observed between

446   opposite-sex and same-sex adult faces (Helmert contrasts, all p > .08).

447

448 Although women tended to show greater LPC responses than men, in

449 general, this sex difference was only significant at 600-650ms ($F(1,24) =$

450 4.69, $MSE = 17.11$, $p = .040$, $\eta^2 = 0.16$), marginally significant at 400-450ms

451 and 500-550ms (both $F(1,24) > 3.49$, both $MSE < 30.07$, both $p < .075$, both

452 $\eta^2 > 0.12$), and failed to reach significance at the remaining time windows (all

453 $F(1,24) < 2.80$, all $p > .10$, all $\eta^2 < 0.10$).

454

455 *Aesthetic* had a significant effect at 300-350ms ($F(1,24) = 4.65$, $MSE = 0.67$,

456 $p = .041$, $\eta^2 = 0.16$) whereby the low-aesthetic versions of the faces elicited

457 higher LPC amplitudes than the high-aesthetic versions of the faces.

458 However, there were no other significant effects of *aesthetic* (all $F(1,24) <$

459 2.76, all $p > .11$, all $\eta^2 < 0.10$). At 300-350ms, there was a three-way

460 interaction between *face type*, *aesthetic*, and *participant sex* ($F(2,48) = 3.29$,

461 $MSE = 0.68$, $p = .046$, $\eta^2 = 0.12$). To explore this interaction, we calculated

462 difference scores measuring the effect of the aesthetic manipulation for each

463 face type by subtracting the LPC response to the low-aesthetic version of

464 each face type, from the corresponding response to the high-aesthetic

465 version. Independent t-tests on these difference scores indicated that

466 although women generally showed a greater difference in response to the

467 high- versus low-aesthetic versions of same sex faces than did men ($t(24) =$

468 1.85, $p = .077$, Bonferroni corrected alpha of .017), there were no *significant*

469 differences with respect to the effect of the aesthetic manipulation on the

470 observed LPC response for any of the face types.

471

472   There were no other significant effects or interactions (all $F < 2.39$, all $p > .10$,

473   all $\eta^2 < 0.09$).

474

475   [INSERT FIGURE 4 ABOUT HERE]

476

477   **Discussion**

478   The current study used an ERP design to investigate the neurophysiological

479   time course of responses to infant and adult faces with varying aesthetic

480   appearance. Using established computer graphic techniques, we directly

481   manipulated attractiveness or cuteness within a given face identity to explore

482   the time course of aesthetic processing in adult and infant faces, respectively.

483   Our behavioral data indicated that there was a perceptible difference in

484   attractiveness (adult faces) or cuteness (infant faces) of the stimuli between

485   the high-aesthetic and low-aesthetic versions. This difference was similarly

486   apparent in men and women for same-sex and infant faces, while the

487   aesthetic manipulation tended to have a greater effect on men's ratings of

488   opposite-sex faces than it did women's. That the degree to which high-

489   aesthetic versions were rated as more attractive/cute than low-aesthetic

490   versions was greater for opposite-sex faces than either same-sex faces or

491   infant faces suggests that facial attractiveness may be particularly salient in

492   potential mates relative to other social groups (e.g., same-sex peers), and is

493   consistent with the commonly observed opposite-sex bias in face processing

494   (e.g., Proverbio et al., 2010b) and face preferences (e.g., Little & Jones 2003).

495

496 Our first aim was to determine whether the preferential response to infant

497 faces previously observed at early processing stages is present at both early

498 and late stages of face processing. Our results demonstrate that both men

499 and women do, indeed, demonstrate enhanced neural responses to infant

500 faces, relative to adult faces, at both early and late stages of processing.

501 Enhanced responses to infant faces relative to adult faces (both same- and

502 opposite-sex) were observed at multiple ERP components, including the N170

503 (amplitude), P2 (amplitude and latency), and LPC. This result is consistent

504 with previous research demonstrating an early (130-170ms) "baby specific"

505 neural response observed in frontal (Kringelbach et al., 2008) and occiptio-

506 temporal regions (Proverbio et al., 2011b). Although Kringelbach et al. (2008)

507 observed this response as early as 130ms, we did not observe a heightened

508 response to infant faces at the P1 component. Our finding is consistent with

509 Proverbio et al. (2011b), who also failed to find a heightened response to

510 infant faces at P1 in occipito-temporal regions. Kringelbach and colleagues

511 (2008) analyzed the alpha and beta oscillatory activity of source generators

512 determined by applying synthetic aperture magnetometry on MEG

513 data. Because modulation of alpha and beta activity by infant faces may not

514 be phase locked to stimulus onset, the early differences reported by

515 Kringelbach and colleagues (2008) may not be evident in our evoked

516 response data. Moreover, our, and most other ERP studies apply low pass

517 filters inconsistent with the analysis of higher frequency oscillatory

518 activity. These methodological differences may explain differences across

519 studies in terms of the earliest detectable "baby specific" response. Both the

520 current study and Proverbio (2011b), however, observed heightened

521   responses to infant faces at the N170 component. Overall, our results

522   demonstrate additional evidence for a "baby specific" early neural response.

523   This type of preferential processing at the early stages of face processing may

524   lead to increased attention and subsequent later processing (Barbeau et al.,

525   2008).

526

527   We also extend these previous findings by demonstrating heightened

528   processing of infant faces, relative to adult faces, at later stages of processing

529   (i.e., the LPC). Given that the LPC reflects attentional or motivational

530   processing (van Hooff et al., 2011) related to the affective value of a stimulus

531   (Johnston & Oliver-Rodríguez, 1997, Schupp et al., 2000; 2004), the

532   enhanced response to infant faces at this stage of processing may suggest

533   that infant faces hold increased attentional or motivational salience relative to

534   adult faces. Indeed, this explanation is consistent with visual attention studies

535   demonstrating that infant faces are attentionally prioritized over adult faces

536   (Brosch et al., 2007; Cárdenas et al., 2013). However, behavioral studies of

537   the motivational salience of infant faces have not necessarily provided

538   converging evidence that infant faces are more motivationally salient than

539   adult faces in general (Parsons et al., 2011a), but they may be more

540   motivationally salient than same-sex faces, at least among heterosexual

541   women (Hahn et al., 2013). Thus, the increased LPC response observed here

542   could be more closely tied to attentional salience than motivational salience.

543   This interpretation would be consistent with our finding that, overall,

544   participants did not rate the baby faces as more attractive than the adult

545   faces.

546

547 Our second aim was to investigate the effects of aesthetic appearance on the

548 processing of adult and infant faces. We observed enhanced responses to

549 low-aesthetic versions of the faces as compared to high-aesthetic versions of

550 the faces at the N170 and P2 components, but not the P1 or LPC. Previous

551 studies suggesting that the attractiveness of adult faces modulates these

552 early components have provided equivocal evidence as to the direction of this

553 effect; several studies have found enhanced responses to atypical or

554 unattractive faces relative to typical or attractive faces (Chen et al., 2012; Halit

555 et al., 2000; Trujillo et al., 2014), while others have observed enhanced

556 responses to attractive faces relative to unattractive faces (Zhang et al., 2011,

557 2012). One possible explanation is that varying appearance within an

558 individual identity (e.g. Halit et al., 2000) produces different effects than using

559 natural variation in appearance (e.g., Zhang et al., 2011). Future work

560 exploring how subtle variation versus naturally occurring variation in aesthetic

561 quality of faces impacts the neural processing of faces may shed light on this

562 issue. Another possibility is that responses may be modulated by deviation

563 from averageness rather than attractiveness, per se, as enhanced responses

564 have been observed for attractive and unattractive faces relative to

565 average faces (Schacht et al., 2008; Trujillo et al., 2014; van Hooff et al.,

566 2011). Indeed, several behavioral studies have demonstrated that the

567 relationship between averageness and attractiveness is complex and non-

568 linear (e.g., DeBruine et al., 2007; Perrett et al., 1994). It may be the case

569 that, in the present study, the unattractive faces were farther from an average

570 (or prototypical) face than were the attractive faces, leading to an increase in

571   the N170 and/or P2 components. Importantly, there was no interaction

572   between aesthetic and face type at either the N170 or P2 component,

573   suggesting that aesthetic appearance may have similar effects on the

574   processing of adult and infant faces.

575

576   Surprisingly, we did not find effects of attractiveness/cuteness for the LPC,

577   with the exception of a single negative relationship at the earliest time window

578   (300-350ms). This late component has previously been shown to respond

579   differentially to attractive and unattractive stimuli, although again the direction

580   is unclear (Chen et al., 2012; Johnston & Oliver-Rodríguez, 1997; Schacht et

581   al., 2008; Werheid et al., 2007). It may be that the aesthetic manipulation we

582   employed here was too subtle to elicit differential responses at the late stage

583   of processing, even though participants could clearly detect differences in

584   attractiveness. If, as Johnston (e.g. Johnston & Oliver-Rodríguez, 1997) and

585   others have suggested, the LPC is sensitive to incentive salience, it is

586   possible that the image set used in our study did not contain faces that were

587   unattractive enough to influence their affective value. As such, although subtle

588   differences in attractiveness were detected, they did not influence the value or

589   salience of the face that is indexed in the LPC. An additional condition in

590   which the faces were manipulated to be unpleasant or highly unattractive

591   would serve as confirmation of this hypothesis. Indeed, there is evidence that

592   facial deformities in infant faces, such as cleft lip, negatively impact upon their

593   incentive salience (Parsons et al., 2011b).

594

595   Finally, we investigated potential sex differences in responses to the aesthetic

596   appearance of adult and infant faces. Consistent with previous findings,

597   (Proverbio et al., 2006b, 2010a, 2011b), women tended to show increased left

598   hemisphere activity compared to men early during processing (as indicated by

599   a right hemisphere bias in men that was absent in women). Interestingly, this

600   was most prominent for the processing of opposite- and same-sex faces and

601   was not apparent for infant faces. Additionally, we found this asymmetry in an

602   earlier ERP component (P1) than has previously been studied (N170;

603   Proverbio et al., 2010a). Proverbio and colleagues, who reported the lack of

604   asymmetry in females for the N170, did not evaluate responses other than the

605   N170, and in a subsequent investigation (Proverbio et al., 2011b) no

606   asymmetries were reported based on evaluation of the scalp electrode ERP.

607

608   We did not find any evidence for a sex difference in the LPC response to

609   infant faces. Although some studies suggest that a sex difference may exist

610   for behavioral and neural responses to infant cues, others present no

611   evidence of such a sex difference in responses to infant cues (reviewed in

612   Hahn & Perrett, 2014). Interestingly, one study found that women show

613   greater responses to infant cues in a sample of parous, but not nulliparous,

614   individuals (Proverbio et al., 2006a), suggesting that parity may influence

615   responses to infant cues. In the present study, women tended to show an

616   increased LPC response to all stimuli types, relative to men, although this

617   difference did not reach statistical significance at all time windows. However,

618   this pattern is consistent with work demonstrating that women show increased

619   responsivity to social stimuli, generally (Proverbio et al., 2008).

620

621 The current study assessed men's and women's responses to the aesthetic

622 quality of adult and infant faces in a sample of young, nulliparous adults.

623 While nulliparous samples are frequently used to assess responses to infants

624 (e.g., Glocker et al., 2009; Hahn et al., 2015a, 2015b), there is some evidence

625 that parental status may modulate neural and behavioral responses to infants

626 (Proverbio et al., 2006a; Weisman et al., 2006; c.f. Noll et al., 2012) and that

627 familiarity with infants can affect early and late processing differently (i.e.,

628 "own" versus "other" infant effects, Bornstein et al., 2013; Esposito et al.,

629 2015). Future work is needed to determine if the enhanced response to infant

630 faces is similar in in nulliparous and parous individuals. A potential limitation

631 of the current study is that we did not account for psychological conditions that

632 may impact the processing of infant cues, such as depression (e.g., Laurent &

633 Ablow, 2012). Additional work is needed to determine if the effects of

634 depressive symptoms affect the processing of adult and infant faces in a

635 similar fashion.

636

637 Overall, our results demonstrate a preferential response to infant faces in

638 early and late processing stages that is independent of the aesthetic quality of

639 the face or observer sex, providing additional evidence for a "baby specific"

640 neural response (e.g., Kringelbach et al., 2008). This "baby specific" neural

641 response may serve an adaptive function – because human infants are highly

642 dependent on caregivers for survival, increased attentional processing of

643 infant stimuli may help to orient adults towards infants. Indeed, previous

644 research has provided evidence for heightened biological sensitivity to infants

645   in mothers (Bornstein et al., 2013), and here we extend this finding to show a

646   similar heightened processing in nulliparous individuals. Given the prevalence

647   of alloparental care in modern society, it would be potentially beneficial for

648   parents and non-parents alike to show increased attentional processing of

649   infant cues.

650

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657

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911

912   **Figure Captions**

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914   *Figure 1.* Examples of high-cute/attractive (left column) and low-cute/attractive (right

915   column) faces.

916

917   *Figure 2.* Average ratings from women (purple bars) and men (blue bars) given to the

918   low-aesthetic versions (dashed) and high-aesthetic versions (solid) of each face type.

919

920   *Figure 3.* N170-responses to infant faces (blue lines), same-sex adult faces (red

921   lines), and opposite-sex adult faces (grey lines). Solid lines represent the high-

922   aesthetic versions of the faces while dashed lines represent the low-aesthetic

923   versions of the faces.

924

925   *Figure 4.* LPC-responses to infant faces (blue lines), same-sex adult faces (red

926   lines), and opposite-sex adult faces (grey lines) from two posterior midline channels.

927   Solid lines represent the high-aesthetic versions of the faces while dashed lines

928   represent the low-aesthetic versions of the faces. The vertical lines beginning at

929   300ms show the borders of the eight analysis windows.

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