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1 **Impaired processing of facial happiness, with or without awareness, in developmental**
2 **prosopagnosia**

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34 **Abstract**

35 Developmental prosopagnosia (DP) is associated with severe, lifelong deficits in face
36 recognition, with such cases often cited as support for a dissociation between the processing of
37 facial identity and emotion. Here we examine the evidence against this dissociation and propose
38 that the processing of facial happiness, either with or without awareness, is actually integrated
39 within the same neural network involved in facial identity recognition. We also test this
40 hypothesis on a group of DP cases and neurotypical controls (NT) by adapting them to
41 expressionless neutral faces, intact happy faces and hybrid faces. Despite these hybrid faces
42 being explicitly identified as expressionless due to their higher spatial frequencies taken from a
43 neutral face, their low spatial frequencies convey happy facial expressions that participants are
44 unaware of. After adaptation, participants were asked to judge the facial expressions of face
45 stimuli that were morphed incrementally in varying degrees of sad through to happy. Both
46 groups exhibited emotion adaptation aftereffects to the intact happy faces, although this effect
47 was smaller in DP. Whereas NT produced emotion adaptation aftereffects without awareness of
48 the happy emotion in the hybrid faces; as a group, those with DP did not. Furthermore, our DP
49 cases also exhibited deficits in judging the emotion of the happiest morphed test faces. Our
50 results indicate that the processing of happy facial expressions, with or without awareness, is
51 likely integrated within the face recognition network. We hypothesize that the previously
52 identified abnormalities in the fusiform gyrus in those with DP is the most likely structure
53 responsible for these deficits.

54

55 **Abstract word count:** 255 words.

56 **Keywords:** Emotion, happy, expression, adaptation, face, spatial frequencies.

57 **Highlights**

58 Processing of facial happiness is impaired in developmental prosopagnosia

59 These impairments persist when processing should occur without awareness

60 Our cases also exhibited deficits in explicitly judging happy expressions

61 We propose that the processing of facial happiness and identity are integrated

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80 **1. Introduction**

81 Prominent models of face perception posit that facial identity processing occurs through
82 brain regions that are distinct from those that process facial emotion (Bruce & Young, 1986;
83 Haxby & Gobbini, 2011; Haxby et al., 2000). According to these models, facial identity
84 perception is accomplished primarily through the occipital face area (OFA; Gauthier et al., 2000)
85 and parts of the fusiform gyrus (otherwise known as the ‘fusiform face area’ due to its
86 specialisation in processing faces, FFA; Kanwisher et al., 1997). By contrast, the superior
87 temporal sulcus (STS; Puce et al., 1998) is thought to separately process facial expressions
88 (Haxby & Gobbini, 2011; Haxby et al., 2000). This distinction between identity and emotion
89 processing has also been interpreted as reflecting relatively static and unchangeable information,
90 such as a face’s identity, in the OFA and FFA, versus more dynamic or changeable aspects of
91 face perception, such as speech and facial expressions, in the STS (Bate & Bennetts, 2015;
92 Haxby & Gobbini, 2011; Pitcher, Duchaine, & Walsh, 2014).

93 More recently, converging behavioural, neuroimaging and neuropsychological evidence
94 has challenged these dissociation models. For example, TMS to the right OFA has been shown to
95 disrupt emotion discrimination (Pitcher, 2014; Pitcher et al., 2008), thus implicating its
96 functional contribution to emotion perception. Similarly, a number of neuroimaging studies have
97 highlighted the FFA’s role in processing facial expressions (Fox et al., 2009; Tsuchiya et al.,
98 2008; Van den Stock et al., 2008). Conversely, the STS has exhibited neural sensitivity to facial
99 identity, both in humans (Fox et al., 2009) and in monkeys (Perrett et al., 1983). These
100 converging findings suggest that contrary to traditional face perception models, emotion and
101 identity perception are integrated across the ‘core’ cortical face perception regions.

102 In contrast to the ‘core’ regions that encompass the OFA, FFA and STS, the amygdala is
103 a subcortical structure that is considered to be an ‘extended’ part of the face perception network
104 (Haxby & Gobbini, 2011). This region is also thought to be highly important in the perception of
105 emotion, regardless of whether the viewer is aware of the emotional information they are
106 viewing or not (Johnson, 2005; Tamietto & De Gelder, 2010). However, amygdala damage has
107 been shown to produce greater levels of impairment in the processing of negative emotions, such
108 as fear and sadness (Adolphs & Tranel, 2004; Adolphs et al., 1994; Adolphs et al., 1999;
109 Anderson & Phelps, 2000; Calder, 1996; Laeng et al., 2010; Vuilleumier et al., 2004). More
110 specifically, amygdala lesions have been shown to entirely spare explicit judgements of facial
111 happiness (Adolphs & Tranel, 2004). This point is bolstered by another study which found an
112 amygdala lesion patient was able to process the low spatial frequencies (LSF; the coarse, holistic
113 visual information conveyed by a face) of happy, but not sad or fearful, facial expressions
114 without conscious awareness (Laeng et al., 2010). These latter two findings are particularly
115 relevant, as they seem to suggest that the amygdala can be redundant in processing happy facial
116 information either with, or without, conscious awareness. Instead, these pieces of indirect
117 evidence hint that facial happiness might be processed through a cortical route that includes the
118 FFA.

119 Direct evidence that facial happiness is processed through the FFA comes from
120 neuroimaging and neuropsychological research. Tsuchiya and colleagues (2008) found that
121 activity in the ventral temporal cortex (which includes the FFA) was associated with the
122 discrimination of facial happiness over fear. Differential neural responses have also been
123 apparent in the FFA of neurotypical individuals viewing happy versus neutral facial expressions
124 (Van den Stock et al., 2008). In the same study, developmental prosopagnosia (DP) cases,

125 individuals who suffer from lifelong impairments in face recognition, had a reduction in their
126 FFA's differential neural activity when viewing these two different facial expressions. These
127 findings not only indicate that the FFA is partly specialised for the processing of facial
128 happiness, but that its ability in DP to distinguish neutral from happy facial expressions might be
129 compromised.

130 DP cases exhibit abnormalities throughout their cortical face perception areas' grey
131 matter volume, connectivity and neural responses to faces (Avidan et al., 2014; Behrmann et al.,
132 2007; Garrido et al., 2009; Gomez et al., 2015; Lohse et al., 2016; Lueschow et al., 2015; Rivolta
133 et al., 2014; Song et al., 2015; Thomas et al., 2008; Zhang et al., 2015). Early studies seemed to
134 indicate that those with DP were spared in their emotion recognition abilities (Behrmann et al.,
135 2007; Dinkelacker et al., 2010; Duchaine et al., 2003; Van den Stock et al., 2008), thus
136 supporting the proposed dissociation between emotion and identity perception. However, recent
137 work employing paradigms designed to be more sensitive in detecting emotion perception
138 deficits have shown that those with DP are indeed impaired when processing facial expressions
139 (Biotti & Cook, 2016; Palermo et al., 2011). However, both of these recent studies collapsed
140 their results across different emotions, making the reader unable to tell which specific emotions
141 the DP cases were impaired in perceiving. If facial happiness is heavily reliant upon the FFA,
142 then those with DP may exhibit a specific impairment in their processing of facial happiness due
143 to their FFA abnormalities.

144 Remarkably, no study to date has shown that DP cases are impaired in their perception of
145 facial happiness or abnormal in their processing of emotion without conscious awareness. The
146 processing of facial emotion without awareness is thought to occur in a qualitatively different
147 way, that is through the amygdala, in contrast to when it is processed with awareness through the

148 cortex (Tamietto & De Gelder, 2010). DP cases have been shown to exhibit amygdala that are
149 typically intact both structurally and in their functioning (Behrmann et al., 2007; Dinkelacker et
150 al., 2010; Van den Stock et al., 2008). If the processing of facial emotion without awareness
151 occurs through this subcortical route as is commonly argued (Tamietto & De Gelder, 2010), then
152 we should expect those with DP to be unimpaired when attempting to process such information.
153 By contrast, if facial happiness were to traverse a cortical route which includes the FFA, then
154 those with DP will likely exhibit impairments in perceiving happy facial expressions.

155 One way that facial happiness processing can be tested in DP is through the use of an
156 emotion adaptation paradigm. After viewing a happy face for a few seconds, subsequently
157 presented faces appear sadder: the so called “adaptation aftereffect” (Wang et al., 2016; Webster
158 et al., 2004). These aftereffects are thought to arise due to neuronal populations specialised in
159 detecting the adaptor’s characteristics (i.e., facial happiness) becoming habituated to this
160 information (Frisby, 1981). Adaptation aftereffects therefore index how well a participant’s brain
161 can process facial happiness. It has recently been shown that adaptation aftereffects can be more
162 sensitive in detecting subtle emotion perception differences than explicit emotion discrimination
163 judgments (Liu, Montaser-Kouhsari, & Xu., 2014; Luo, Burns, & Xu, 2017). In this respect,
164 adaptation paradigms are actually a better way of examining emotion perception in DP cases
165 who might otherwise falsely evince neurotypical processing of emotion through explicit
166 recognition tasks (e.g., Duchaine et al., 2003; Palermo et al., 2011).

167 Numerous studies have previously examined conscious awareness and face adaptation
168 (Adams, Gray, Garner, & Graf, 2010; Amihai, Deouell, & Bentin, 2011; Moradi, Koch, &
169 Shimojo, 2005; Shin, Stolte, & Chong, 2009; Stein & Sterzer, 2011; Yang, Hong, & Blake,
170 2010). We recently showed that a hybrid face, whereby a happy facial expression in the hybrid’s

171 LSF was masked from participants' awareness by the higher spatial frequencies of a neutral face,
172 was still able to produce similar emotion adaptation aftereffects as those induced by intact happy
173 faces in neurotypical participants (Burns et al., submitted). If we were to observe diminished or
174 non-existent emotion adaptation aftereffects in DP to either an intact happy or neutral-happy
175 hybrid face, then it would imply that their neuronal populations involved in detecting facial
176 happiness are not performing as they should be.

177 The first aim of the present study was to test whether individuals with DP can process
178 happy facial emotion, with or without conscious awareness, in a neurotypical manner.
179 Remarkably, no prior study has examined emotion processing without awareness in DP, despite
180 awareness typically being argued as modulating how facial emotions are processed in
181 qualitatively different ways (Tamietto & De Gelder, 2010). To test this, we employed an emotion
182 adaptation paradigm whereby a group of DP cases and controls were adapted to intact neutral
183 faces, intact happy faces, and hybrid faces (Laeng et al., 2010; Schyns & Oliva, 1999). Figure 1
184 gives examples of the stimuli used and the experimental procedure. While our participants will
185 be aware of the emotion conveyed by the happy faces, they will not be aware of the happy
186 emotion conveyed by the hybrids' LSF due to the remaining spatial frequencies conveying a
187 neutral expression (Laeng et al., 2010). As DP cases have abnormalities in their grey matter
188 volume throughout their cortical face perception network including the FFA, we anticipate that
189 they should exhibit non-existent or diminished emotion adaptation aftereffects to the hybrid, and
190 possibly intact happy, faces. Such a result would imply that the processing of the LSF of happy
191 facial emotion is reliant upon the face recognition network due to associative face recognition
192 deficits in DP. By contrast, if our DP cases were to exhibit neurotypical adaptation aftereffects to
193 the happy and hybrid faces, then it would suggest that emotion processing is dissociable from

194 that of identity. A second aim of our study was to test whether DP cases' also experience
195 impairment in explicitly judging facial happiness. To assess this, we examined our DP cases'
196 consistency, sensitivity and response times when making judgments of emotion to our test faces.

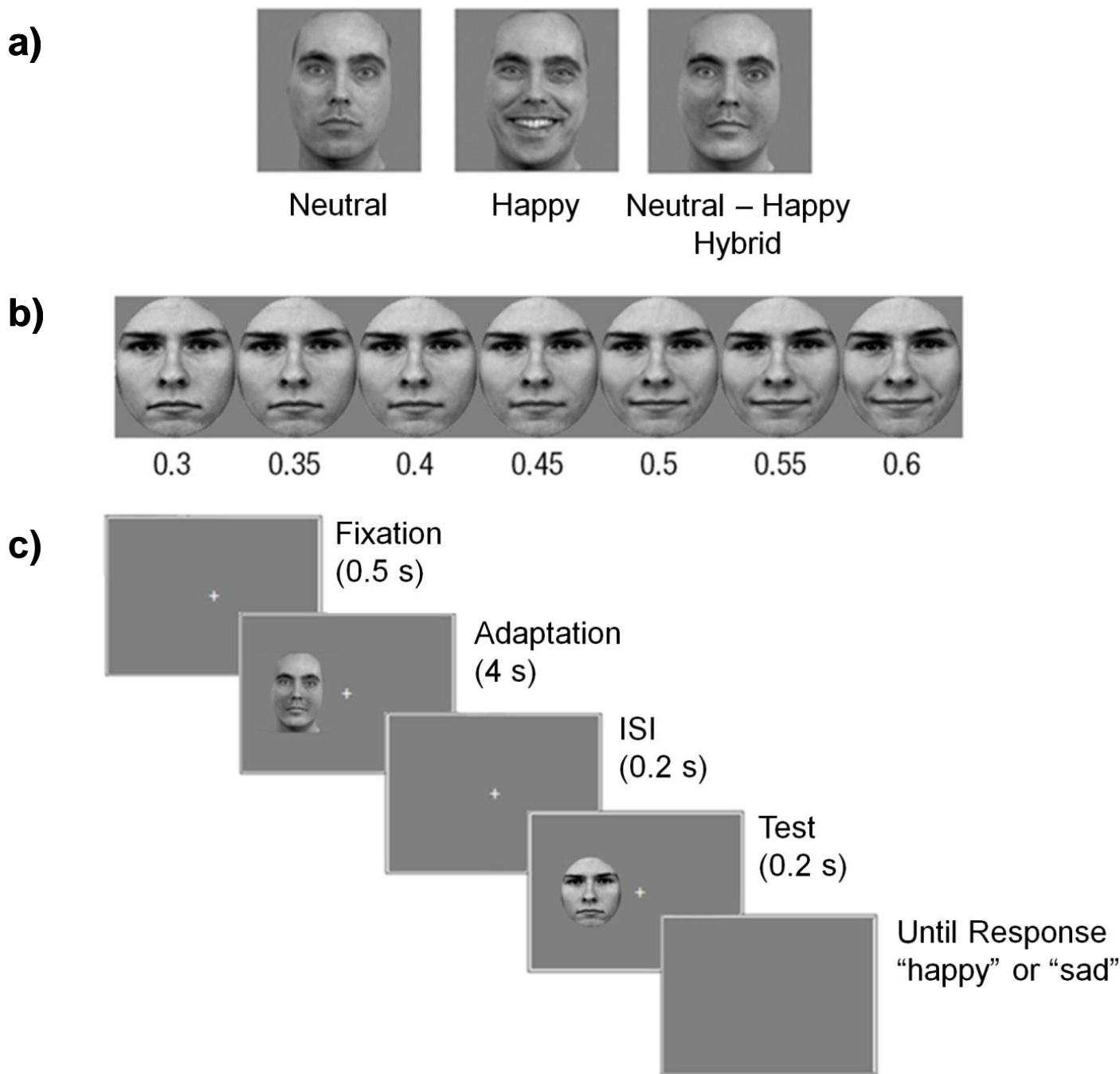
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198 **2. Methods**

199 *2.1. Participants*

200 Ten controls and 10 DP cases (both groups had 3 males) participated in this experiment.
201 The controls were matched to the DP cases for gender, ethnicity and roughly their age: control
202 range 20-40 years (mean age 28.5 years) with the DP range 19-46 years (mean age 29 years). All
203 participants had normal or corrected to normal vision and were compensated financially for their
204 time. The study was approved by the Institutional Review Board at Nanyang Technological
205 University, Singapore. While the controls did not complete our neuropsychological tests for face
206 processing impairment, none of them reported difficulties in recognising faces when asked a
207 series of questions designed to probe their experiences with faces.

208 DP cases were recruited via faceblind.org, email appeals within Nanyang Technological
209 University, or after responding to a prosopagnosia piece in local newspapers. All DP cases then
210 underwent an interview with the first author confirming their regular difficulties with faces.
211 Table 1 displays the DP cases that participated in the experiment and their neuropsychological
212 test results for face processing impairment. The Famous Faces Test (FFT; Duchaine &
213 Nakayama, 2005) typically consists of 60 celebrity faces which the participant is required to
214 name or identify in some way; neurotypical performance on this test is usually around 90%
215 correct (SD = 5%; Duchaine et al., 2007). We employed two shortened versions of a famous



216

217 Figure 1. Examples of Stimuli and Trial Sequence. a) Three different adapting stimuli for one of
 218 the two identities (from left to right): intact neutral face, intact happy face, and the neutral-happy
 219 hybrid face. b) Test faces ranging in proportion of happiness from 0.3 through to 0.6. c) Example
 220 of trial sequence, taken from the second identity’s hybrid face block. A fixation first appears on
 221 the screen for 0.5 s. The adapting face image would then be displayed for 4 s followed by an
 222 inter-stimulus interval (ISI) that lasted 0.2 s. A test face would then appear for 0.2 s before being
 223 replaced by a response screen whereby participants had to press either the happy (“A”) or sad
 224 (“S”) key to indicate the emotion of the test face and move onto the next trial.

Participants	Age	Ethnicity	Sex	FFT (%)	CFMT z	CFPTupr Z	CFPTinv z
DP1	20	Chinese	F	53	-2.95	-1.36	-2.32
DP2	21	Chinese	F	24	-2.95	-1.54	-2.47
DP3	46	Caucasian	M	37	-3.66	0.22	-0.8
DP4	19	Chinese	F	24	-2.12	-2.22	-1.69
DP5	28	Caucasian	F	42	-2.01	-1.75	1.62
DP6	39	Chinese	F	32	-3.3	-0.16	-0.03
DP7	22	Chinese	M	45	-2.12	-1.19	-0.03
DP8	23	Chinese	F	63	-2.47	-2.4	-1.07
DP9	30	Caucasian	F	32	-3.15	-0.93	-0.08
DP10	37	Chinese	M	53	-3.18	-1.71	-0.91

233
234 Table 1. Neuropsychological test results of the 10 DP cases that participated in the experiment.
235 The age, ethnicity and gender of each participant can be gleaned from the second, third and
236 fourth columns. The remaining columns indicate: Famous Faces Test (FFT), Cambridge Face
237 Memory Test (CFMT: the original was used for Caucasian participants, Asian for Chinese),
238 Cambridge Face Perception Test upright and inverted (CFPTupr and CFPTinv).

239
240 faces test, each containing 38 items: one with famous faces that local Chinese participants would
241 recognise and another for our Caucasian participants. Table 1 shows that all of the DP cases were
242 impaired at recognising famous faces.

243 The Cambridge Face Memory Test (CFMT; Duchaine & Nakayama, 2006) requires the
244 participant to memorise 6 target Caucasian faces presented in a number of different views; these
245 faces must then be identified when displayed individually with two distractor faces. Our
246 Caucasian DP cases completed the original version of the CFMT whereas our Chinese cases
247 completed a version of this task which consists of Chinese faces instead (McKone et al., 2012).
248 As with the famous faces, all of our DP cases were impaired (i.e., more than 2 SDs below the
249 control mean) on this task.

250 During the Cambridge Face Perception Test (CFPT; Duchaine et al., 2007), participants
251 are shown a target face presented in three-quarter view along with 6 faces presented in frontal
252 view; these 6 faces have been morphed to appear similar in varying percentages to the target

253 face. Participants are required to arrange the faces in order of similarity to the target face. The
254 test displays faces either upright or inverted. As there is no Chinese version available for this
255 test, we collected normative scores from a local Chinese sample ($N = 12$) to see whether
256 performance on this task can be comparable regardless of ethnicity. Remarkably, the Chinese
257 scores on the upright ($M = 32.2$, $SD = 11.6$) and inverted ($M = 62.3$, $SD = 12.8$) portions of this
258 task were almost identical to previous studies of Caucasians (Bowles et al., 2009; Duchaine,
259 Germine et al., 2007; Garrido et al., 2008). To our knowledge, this is the first time that the CFPT
260 has been shown to be comparable between the neurotypical Caucasian and Chinese populations.
261 This is in contrast to the CFMT which elicits stark differences across Chinese and Caucasian
262 populations (McKone et al., 2012), with both experiencing the other race effect; that is, better
263 performance for their own race (Chiroro et al., 2008).

264 It may initially seem that these results confirm the CFPT's validity in detecting face
265 perception deficits in ethnic Chinese. However, it may be possible that our neurotypical Chinese
266 participants were using domain general perceptual processes (Furl, Garrido, Dolan, Driver, &
267 Duchaine, 2011) that are in some way distinct from the face-related processes employed by their
268 Caucasian counterparts. Support for this point comes from the lack of an other race effect, that is,
269 poorer performance in our Chinese participants when processing Caucasian faces on the CFPT in
270 comparison to Caucasians in the literature (Bowles et al., 2009; Duchaine, Germine et al., 2007;
271 Garrido et al., 2008). This argument, however, does seem countered by the fact that our Chinese
272 participants exhibited an inversion effect (Yin, 1969), that is, better performance when faces are
273 presented upright versus inverted: a classic index of face-related processing (Valentine, 1988). If
274 our participants were using domain general processes on this task, then we would expect to see
275 little difference between upright and inverted performance; an outcome that was not realised

276 here. While our Chinese participants do not seem worse than Caucasians on the CFPT, the lack
277 of a Chinese version of this task makes it difficult to confirm whether our Chinese cases would
278 exhibit an other race effect on the CFPT. Thus, any interpretation of this data should be taken
279 with caution. The creation of a Chinese CFPT, however, would certainly be beneficial for
280 diagnosing apperceptive prosopagnosia cases in ethnic Chinese. Table 1 shows that only two
281 cases were abnormal on the CFPT. Keeping in line with previous DP research (Bate et al., 2014;
282 Burns et al., 2014), however, our criteria for identifying DP cases required impairment on both
283 the CFMT and FFT.

284 2.2. Stimuli

285 Adapting stimuli consisted of 6 different images: four taken from the Radboud Faces
286 Database (Langner et al., 2010), with the remaining 2 adaptors consisting of hybrid faces. The 4
287 images from the Radboud Database comprised of 2 images taken from 2 different facial
288 identities, with one identity shown in Figure 1a. The reason for using 2 facial identities was to
289 ensure any possible effects found were robust, replicable, and due to the emotional content
290 conveyed by the LSF, rather than some aberrant visual property that might be apparent in a
291 single face image. For each identity, one adaptor was merely an image of the face posing a
292 neutral expression. The second adaptor was the same individual in a happy expression. The
293 hybrid adaptor was a neutral-happy hybrid, created by blending the higher spatial frequencies of
294 the neutral face (7-128 cycles/image) with the LSF from the happy face (1-6 cycles/image) of the
295 same identity (Laeng et al., 2010; Prete et al., 2015). The happy face from the first identity was
296 low-pass filtered to obtain the LSF (1-6 cycles/image). The hair and ears were cropped from each
297 of the faces using the lasso tool in Adobe Photoshop, and the resulting images were matched for

298 luminance using the SHINE toolbox (Willenbockel et al., 2010) for MATLAB. The above
299 method was repeated for the second identity.

300 Test stimuli images in Experiment 1 (Figure 1b) were created from three black and white
301 photographs of one person posing a sad, happy, or neutral expression in a full frontal facing
302 position to the camera, taken from the Karolinska Directed Emotional Faces (KDEF; Lundqvist
303 et al., 1998) database. These images were then cropped to remove all extraneous information.
304 Using Morph Man 4.0 (STOIK Imaging, Moscow, Russia) software, we averaged either the sad
305 to neutral face images or the neutral to happy face images to generate 21 images with proportion
306 of happiness from 0 (saddest) to 1 (happiest) in incremental steps of 0.05 (the 0.5 face
307 represented the neutral face). Test stimuli comprised 7 of these faces reflecting incrementally
308 increasing proportions of happiness: 0.3, 0.35, 0.4, 0.45, 0.5, 0.55, and 0.6 happy face
309 proportions. We chose test faces from a different face identity from the adapting faces for a
310 number of reasons: 1) to remove any effect of the same identity giving our controls a
311 differentially larger boost to emotion adaptation aftereffects (Fox & Barton, 2007) in comparison
312 to our DP cases who obviously have deficits in processing identity; 2) previous research has
313 found that emotion adaptation can still transfer across different identities (Fox & Barton, 2007).

314 The stimuli were presented on a 15.6" computer monitor screen, to the left of a fixation
315 cross as shown in Figure 1, with a center-to-center distance of 4.3° . The computer screen was
316 approximately 60cm from the participant's face, with the adapting stimuli subtending horizontal
317 and vertical visual angles of 3.8° and 5.7° respectively. The test face stimuli subtended
318 horizontal and vertical visual angles of 4.5° and 5.2° respectively. Despite our adaptor and test
319 faces covering roughly the same area on the screen, the unmasked test faces were actually larger
320 than the adapting faces. This incongruence in actual face size between the test and study faces

321 has been used in other adaptation paradigms to reduce retinotopic adaptation (Burton et al., 2015;
322 Rhodes et al., 2015). The vertical refresh rate was 60 Hz, and the spatial resolution was 1366 ×
323 768 pixels. All face stimuli were presented against a grey background. The whole experiment
324 was run using E-Prime 2.0.

325 *2.3. Procedure*

326 The experiment comprised 3 blocks for each identity. Each block displayed one of the 3
327 different adaptor types: intact neutral face, intact happy face and neutral-happy hybrid face. For
328 example, in the happy face adaptation block, the happy face image was presented during every
329 trial as the adaptor stimulus. The blocks for each identity were presented in a random order.
330 Once participants completed the 3 blocks for one identity, they were then required to complete
331 the 3 blocks for the other identity. The choice of which identity was displayed first was chosen at
332 random for each participant. Breaks between blocks lasted roughly the same duration (~5
333 minutes) as a single block.

334 Figure 1c shows the trial sequence for the experiment. Participants started each block of
335 trials by fixating on a central cross and then pressing the space bar. A 500 ms fixation cross
336 would commence every trial. Participants would then see the adapting face appear to the left of
337 the fixation cross for 4 s. The adapting face would disappear during a 200 ms inter-stimulus
338 interval, leaving only the fixation cross. Then followed a test face presented at the same location
339 as the adapting face for 200 ms. Finally, a blank screen was displayed where participants had to
340 judge whether the test face was happy or sad. The participant's response would end that trial and
341 start the next one. There was no feedback on performance provided to the participants at any
342 time throughout the experiment. Each test face was presented in each block 7 times, giving a
343 total of 49 trials in each block.

344 After the whole experiment was finished, we asked participants to judge the emotional
345 expression conveyed by each adaptor as either happy or neutral: all participants (100%)
346 identified the intact happy faces as happy, and the neutral and hybrid faces as neutral. Therefore,
347 the participants were aware of the emotion of the intact happy and neutral adapting faces, but
348 were unaware of the happy emotion conveyed by the hybrid adaptors.

349 Participants were requested to fixate on the centrally presented cross at all times, and to
350 never look directly at the faces, as they were told that the experiment was designed to test how
351 well they could process faces in their visual periphery. Stimuli were presented in the left visual
352 field for a number of reasons. First, faces presented in this area are mainly processed in the
353 contralateral brain hemisphere (Hemond, Kanwisher, & De Beeck, 2007; Towler & Eimer,
354 2015). This is important as prior work has identified the right FFA as being associated with the
355 processing of facial identity (Rotshtein et al., 2005; Schiltz et al., 2006) and facial happiness
356 (Fox et al., 2009; Tsuchiya et al., 2008; Van den Stock et al., 2008), plus those with DP exhibit
357 reduced grey matter volume in their right fusiform gyrus (Garrido et al., 2009). We therefore
358 anticipated that any difficulties in processing emotion in DP would be particularly apparent
359 through the right hemisphere's cortical route. Secondly, it has been suggested that those with DP
360 have difficulties processing facial emotion in a holistic fashion (Palermo et al., 2011). Faces
361 identified in the visual periphery should be more heavily reliant upon the blurry, LSF, which are
362 thought to drive holistic processing (Goffaux et al., 2005; Goffaux & Rossion, 2006). A
363 paradigm that presents faces in the visual periphery should therefore reveal a deficit in the
364 recognition of facial happiness in DP that was not apparent in recent studies where participants
365 could view the faces with high visual acuity in the fovea (Biotti & Cook, 2016; Palermo et al.,
366 2011).

367 We did not record eye-tracking data to test participant adherence to viewing the fixation
368 cross, but we did when using a similar paradigm in a recent publication (Luo et al, 2017). In our
369 other study, stimuli were also presented in the visual periphery with participants required to
370 maintain fixation on a central fixation cross (Luo et al, 2017). We found that the amount of time
371 that a participant broke fixation did not affect the strength of the adaptation aftereffect across 6
372 different conditions (Luo et al, 2017). The same study also found that participants broke fixation
373 less than 3% of the time. We performed between samples *t*-tests on the magnitudes of the
374 aftereffects to the two happy adaptors presented in our other study to our control group's
375 aftereffects to the intact faces here; these results yielded no significant differences [$t(38) = 1.57$,
376 $p = .11$ and $t(38) = 1.01$, $p = .32$]. Therefore, similar sized aftereffects between these
377 experiments indicate that the controls in the present experiment were unlikely to have been
378 viewing the fixation cross in an abnormal way. While DP cases have recently been shown to
379 exhibit aberrant viewing patterns of faces (Bobak, Parris, Gregory, Bennetts, & Bate, 2017),
380 there is nothing in the literature that would indicate they are abnormal in their ability to adhere to
381 viewing a fixation cross. Based on these facts, we do not believe that any differences found
382 between our groups here can be attributed to abnormal viewing behaviours in our DP cases.

383 *2.4 Data Analysis*

384 To measure emotion adaptation aftereffects, we first calculated the proportion of happy
385 responses for every test face in each adaptation condition. The proportions of happy responses
386 were then plotted against the morphed proportions of happiness in the test faces. The results were
387 then fitted with a sigmoidal function in the form of $f(x) = 1/[1+e^{-a(x-b)}]$, where b equals to the 50%
388 point of the psychometric function [the point of subjective equity (PSE)] indicating chance
389 performance, and $a/4$ determines the slope and indicates the response sensitivity. As PSE values

390 reflect the point at which perception of emotion becomes uncertain in any particular condition
391 for each participant, they can therefore be used to test differences between comparable levels of
392 perception across conditions and groups. These comparisons can only be made so long as a
393 certain level of accuracy is achieved in order to fit a reliable psychometric curve on the data,
394 something that was possible with all of our participants' results. However, while the PSE
395 calculation is reliant upon a certain level of accuracy, they can still compare the points at which
396 perception performance is matched between two different groups, even if the groups differ in
397 their general judgment consistency as indicated by the slopes of their curves. Similar studies
398 have used PSE values as a reliable index to compare neurotypical and neuropsychological
399 populations (Cook, Brewer, Shah, & Bird, 2013; 2014). The magnitude of the aftereffect was
400 calculated by subtracting the PSE of the baseline (neutral face adaptation) from the adaptation
401 condition(s) of interest. We conducted mixed models Analysis of Variance (ANOVA) to
402 compare different conditions, and then used two-tailed independent samples *t*-tests (with
403 Bonferroni corrections) to follow up on any significant interactions. All analyses were performed
404 in Matlab or SPSS.

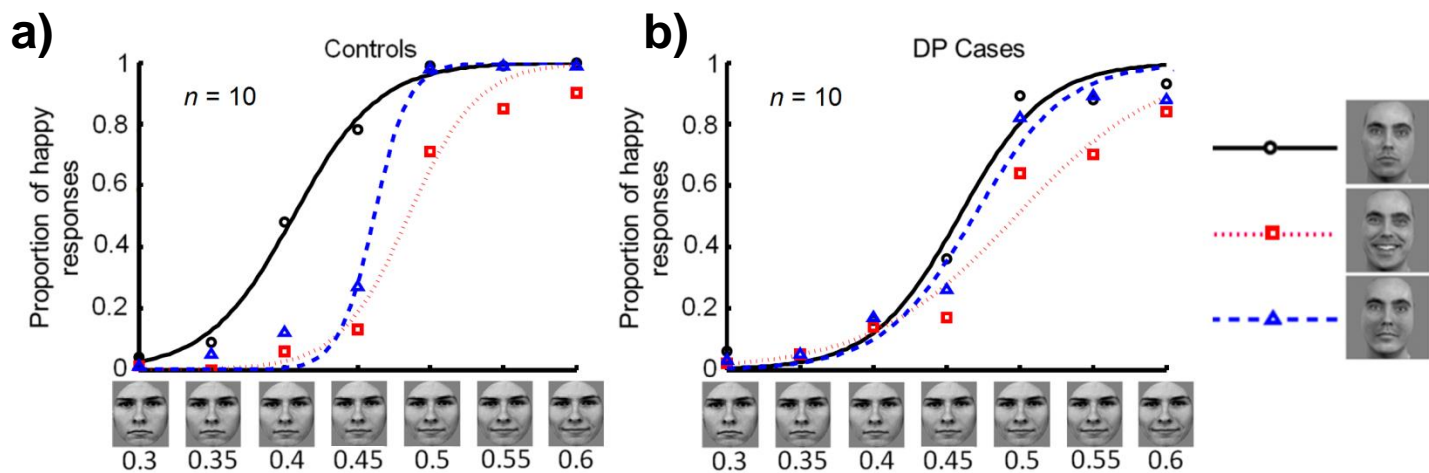
405

406 **3. Results**

407 *3.1. Point of Subjective Equality*

408 To quantify and compare the perception of the adaptors' emotions, we calculated the
409 point of subjective equality (PSE: the proportion of happiness in test stimuli that corresponds to
410 50% happy responses) from the participants' psychometric curves (details in *Data Analysis*
411 section). The average judgements made by all control and DP participants to the test faces after

412 adaptation to the neutral, happy and hybrid adaptors are shown in Figure 2. The controls’
 413 psychometric curves after adapting to the neutral, intact happy and hybrid faces seem to differ in
 414 PSE. Larger PSE values suggest participants require a greater proportion of facial happiness in
 415 the test faces before they can judge a face as happy. The shift between the curves of the intact
 416 happy and hybrid face adaptation from the neutral face condition indicates an adaptation
 417 aftereffect (more details in the *Emotion adaptation aftereffects* section). In comparison, the
 418 differences between these curves for the DP cases are smaller than the controls. The main
 419 difference between the two participant groups is in the psychometric curve of the neutral face
 420 adaptation. For example, for the same test face near the 0.45 proportion of happiness, the
 421 controls judged it as a happy face (black circle in Figure 2a), but the DP cases judged it as a sad
 422 face (black circle in Figure 2b). This suggests that the DP cases have a higher threshold for
 423 judging the test faces as being happy. Such differences do not seem so apparent between the DP
 424 cases and controls in the happy and hybrid conditions.



427
 428 Figure 2. Mean psychometric functions to adaptation from a) neurotypical control participants
 429 (left panel) and b) DP cases (right panel). Black lines = neutral face adaptation, red dotted lines =
 430 intact happy face adaptation, blue dashed lines = hybrid face adaptation.

431 To examine the differences in PSEs between our two participant groups, we performed a
432 $2 \times 2 \times 3$ mixed model ANOVA comprising within subject factors of Identity (1 vs. 2) and
433 Adaptor (neutral vs. happy vs. hybrid), and a between subject factor of Group (controls vs. DP
434 cases) on the raw PSE values. A significant Group effect [$F(1,18) = 8.91, p = .008, \eta^2 = .33$] was
435 found, with the DP cases ($M = .478$) exhibiting a larger PSE overall relative to the controls (M
436 $= .453$). This suggests that the DP cases generally rated the test faces less frequently as happy.
437 There was also a significant main effect for Adaptor [$F(2,36) = 38.34, p < .001, \eta^2 = .68$]. Post-
438 hoc tests with Bonferroni corrections for multiple comparisons revealed that this was due to the
439 happy [$p < .001, M = .499, \text{Cohen's } d = 1.82$] and hybrid [$p < .001, M = .464, \text{Cohen's } d = 1.15$]
440 faces producing larger PSEs relative to the neutral condition ($M = .433$), with the happy adaptor
441 producing the largest of these effects [$p < .001, \text{Cohen's } d = 1.46$] (red dotted line in Figure
442 2a&b). This suggests that test faces were identified as sad more frequently following adaptation
443 to the happy and hybrid faces relative to the neutral faces, and that these adaptation aftereffects
444 were strongest in the happy condition. There was no significant main effect of Identity [$F(1,18)$
445 $= .17, p = .68, \eta^2 = .009$].

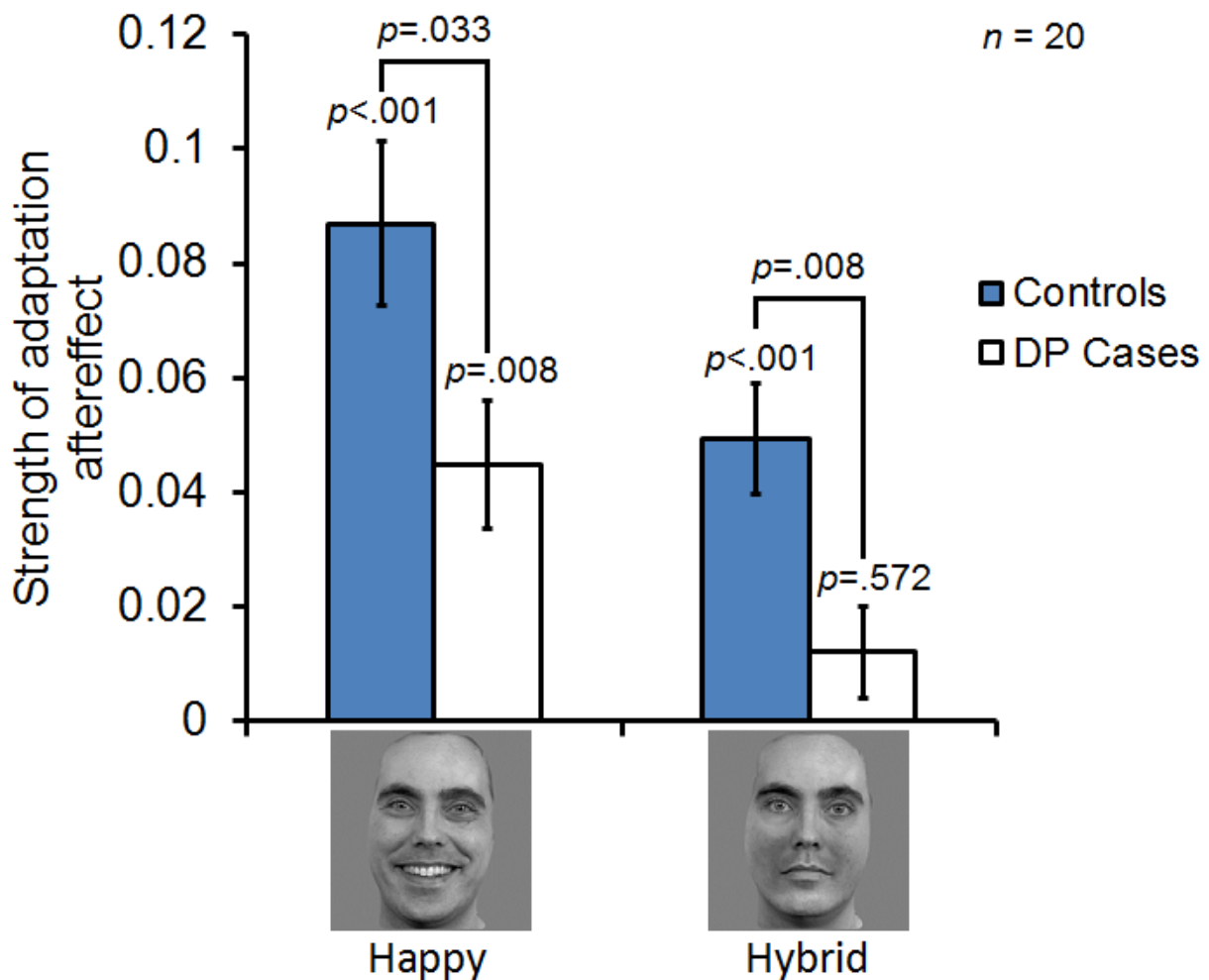
446 There were no significant interaction effects for Group \times Identity \times Adaptor [$F(2, 36) =$
447 $.003, p = .99, \eta^2 < .001$] or Group \times Identity [$F(1, 18) = 1.2, p = .29, \eta^2 = .063$]. By contrast,
448 there was a significant Adaptor \times Identity interaction [$F(2, 18) = 3.97, p = .028, \eta^2 = .18$].
449 Bonferroni corrected *post hoc* comparisons indicated that this was due to a non-significant trend
450 [$p = .078, \text{Cohen's } d = .54$] for the PSE after adapting to the second identity's happy face ($M =$
451 $.51$) being slightly larger than the PSE after adapting to the same condition for the first identity
452 ($M = .49$).

453 Importantly, there was a significant Group \times Adaptor interaction effect [$F(2,36) = 4.69$, p
454 $= .016$, $\eta^2 = .21$] on the raw PSE values. Subsidiary Bonferroni corrected comparisons revealed
455 that the DP cases' PSE values ($M = .459$) were more positive after adapting to the neutral faces
456 relative to the controls ($M = .407$) [$p = .001$, Cohen's $d = 1.79$], with a similar, albeit non-
457 significant [$p = .07$, Cohen's $d = .87$], trend in the hybrid condition (DP cases $M = .471$ vs.
458 controls $M = .457$). By contrast, the PSE values were not different between the two groups after
459 adapting to the happy faces (DP cases $M = .504$ vs. controls $M = .494$) [$p = .5$, Cohen's $d = .3$].
460 Further comparisons identified that for the control participants, the happy [$p < .001$, Cohen's $d =$
461 2.69] and hybrid [$p < .001$, Cohen's $d = 1.64$] faces produced larger PSE values relative to the
462 neutral condition, with the happy adaptor producing the largest of these effects [$p = .004$,
463 Cohen's $d = 1.5$]. This suggests that the controls identified test faces as sad more frequently
464 following adaptation to the happy and hybrid faces, thus indicating the presence of adaptation
465 aftereffects in both conditions. In contrast to the controls, only the DP cases' happy adaptation
466 condition produced larger PSEs in comparison to the neutral [$p = .008$, Cohen's $d = 1.44$] and
467 hybrid condition [$p = .011$, Cohen's $d = 1.06$]; the hybrid and neutral conditions were
468 indistinguishable [$p = .57$, Cohen's $d = .61$]. This indicates that DP cases only identified the test
469 faces as sad more often following the happy adaptor, relative to the neutral and hybrid
470 conditions.

471 *3.2. Emotion adaptation aftereffects*

472 Facial emotion aftereffects were calculated by subtracting the PSE of the neutral face
473 conditions from the happy or hybrid conditions. These aftereffect magnitudes would allow us to
474 compare differences in adaptation aftereffects between the two groups. As we previously found
475 no significant effects or interactions involving Identity between the groups, we averaged the PSE

476 values of both identities together. Figure 3 shows the magnitudes of these aftereffects, with
 477 larger values reflecting greater emotion adaptation relative to the baseline neutral condition. To
 478 compare the magnitudes of these aftereffects between the groups, we performed a 2×2 mixed
 479 model ANOVA employing a within participant factor of Adaptor (happy vs. hybrid), and a
 480 between participant factor of Group (controls vs. DP). We found a significant main effect of
 481 Adaptor [$F(1,18) = 25.93, p < .001, \eta^2 = .59$], indicating that both groups exhibited larger
 482



483
 484 Figure 3. The magnitudes of the emotion adaptation aftereffects for both the controls (filled blue,
 485 $n = 10$) and DP cases (filled white, $n = 10$). The bars on the left represent the aftereffects to the
 486 happy face with the bars on the right showing the aftereffects to the hybrid faces. Comparisons
 487 for each condition are Bonferroni corrected, with p-values for each individual bar a paired
 488 comparison with the neutral baseline condition. Error bars indicate \pm SEM.

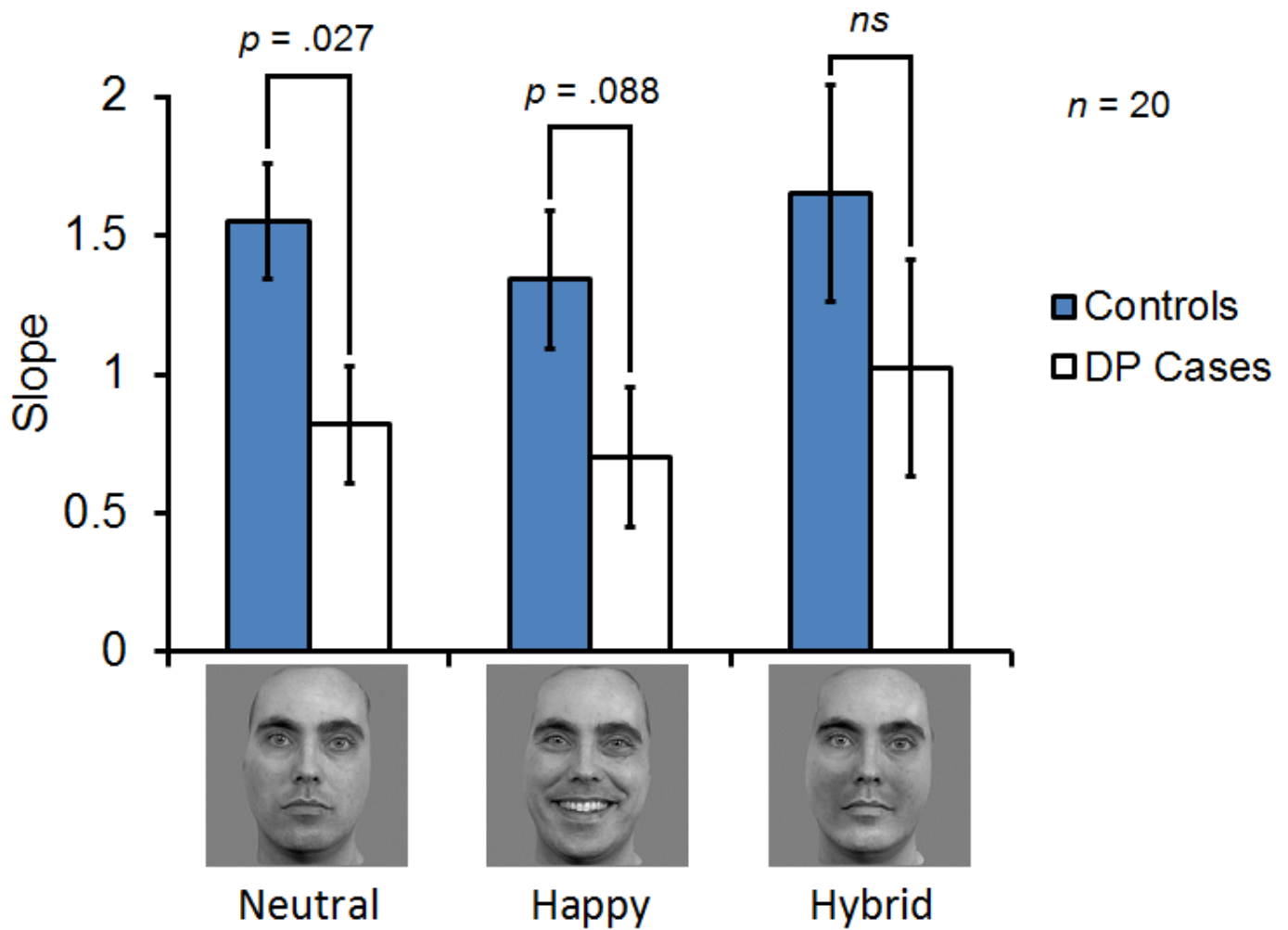
489 aftereffects to the happy adaptors ($M = .066$) compared to the hybrids ($M = .031$). A significant
490 effect of Group [$F(1,18) = 8, p = .011, \eta^2 = .31$] was also revealed due to the controls ($M = .068$)
491 exhibiting greater adaptation aftereffects regardless of condition in comparison to the DP cases
492 ($M = .028$). However, no significant Group \times Adaptor interaction [$F(1,18) = .12, p = .74, \eta^2 =$
493 $.007$] was found. In summary, DP cases displayed diminished adaptation aftereffects to the
494 happy and hybrid faces relative to the controls. These diminished effects appear similar across
495 both groups for both the happy (Mean difference of FEA = $.042$) and hybrid adaptors (Mean
496 difference in FEA = $.037$), indicating an underlying abnormality in our DP cases' abilities to
497 process emotional information conveyed by the LSF of both adaptor types. Instead, it would
498 appear that the ability to produce emotion adaptation aftereffects to the happy adaptor in DP
499 must be due to information conveyed by the higher spatial frequencies (i.e. > 6 cycles/image).

500 3.2. Sensitivity to emotion in the test faces

501 To comprehensively examine any emotion sensitivity deficits in DP to the test faces, we
502 calculated the slope values of the psychometric curves for each adaptor (details in our *Data*
503 *Analysis* section). Our slope values index our participants' general sensitivity at discriminating
504 the two emotions (Liu, Montaser-Kouhsari, Xu, 2014), which is a similar way of examining
505 emotion recognition performance as found in Biotti and Cook's (2016) study. As can be seen
506 from Figure 2, the control participants' slopes for all adaptors appear steeper than the DP cases'
507 slopes. Our calculated slope values are presented in Figure 4, with larger values indicating
508 steeper slopes and better sensitivity at judging the emotions of the test faces. We performed a $2 \times$
509 3 mixed model ANOVA on the slope values, with a within subject factor of Adaptor (neutral,
510 happy, hybrid) and a between subject factor of Group (controls vs. DP). There was a close to
511 significant effect with a medium to large effect size for Group [$F(1,18) = 4.41, p = .05, \eta^2 = .2$]

512 due to the controls' psychometric curve slopes ($M = 1.51$) in Figure 2 being steeper in contrast to
 513 the DP cases ($M = .85$), suggesting that the controls may be more sensitive in emotion judgment.
 514 However, no significant effect [$F(2,36) = .94, p = .4, \eta^2 = .1$] or interaction [$F(2,36) = .023, p =$
 515 $.98, \eta^2 = .003$] involving Adaptor was found.

516



517

518 Figure 4. The slope values for controls (filled blue, $n = 10$) and DP cases (filled white, $n = 10$).
 519 The bars on the left represent the slope after adapting to the neutral face, the bars in the middle
 520 the happy face, and the bars on the right the hybrid faces. Larger values suggest better sensitivity
 521 at judging emotion. Error bars indicate \pm SEM. Between group comparisons are Bonferroni
 522 corrected with p values $< .1$ reported.

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525 3.3. *Consistency in judgments of emotion*

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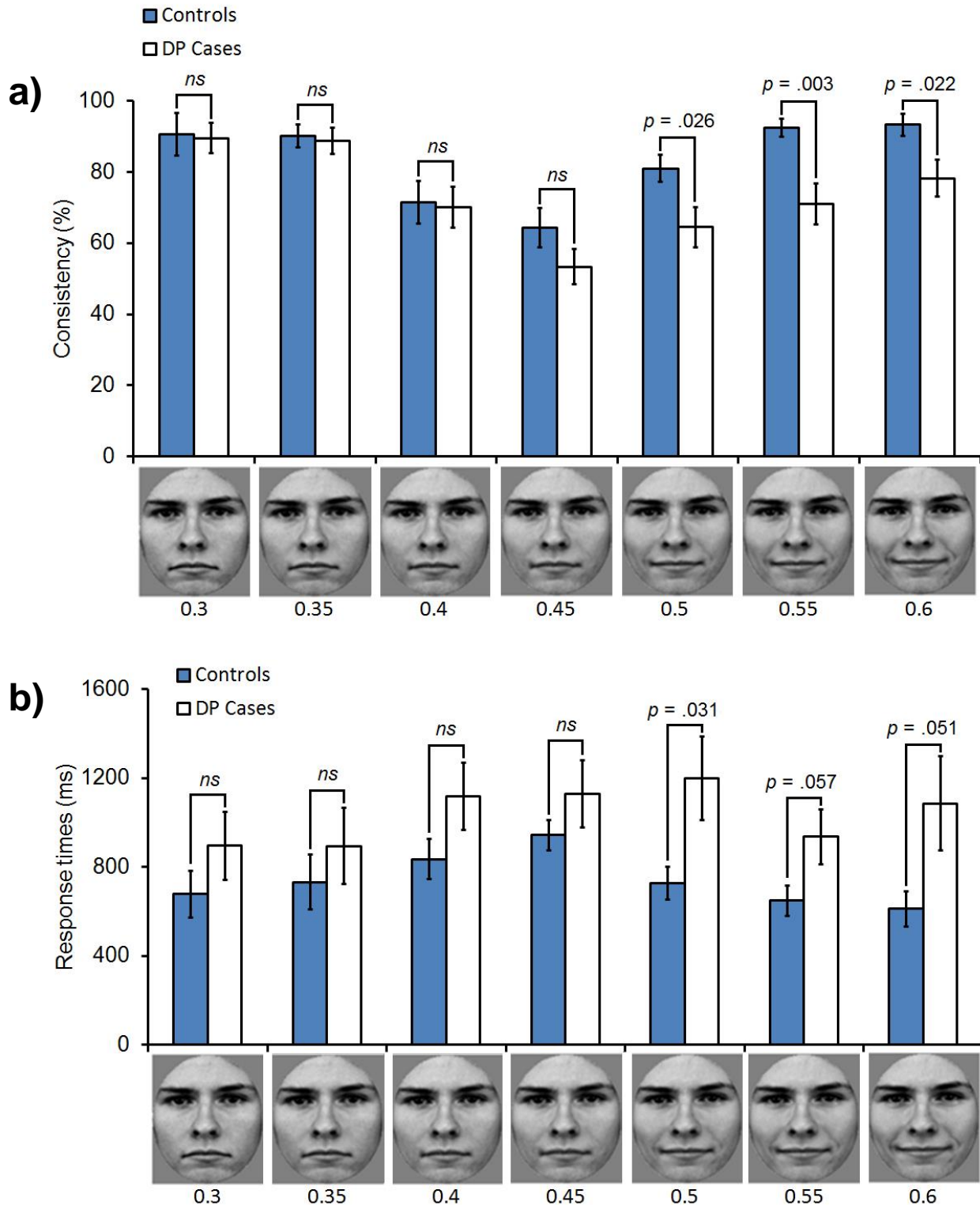
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As mentioned earlier, previous work showing emotion processing impairments in DP have not identified which specific emotions are driving these impairments (Biotti & Cook, 2016; Palermo et al., 2011). To examine whether the trend for a flatter slope in DP was due to difficulties or uncertainty in judging the happiest test faces' emotions as we earlier predicted, we adjusted the proportion of each participant's happy responses for the test faces in each adaptor condition to give us a judgment consistency score. As the proportion of happy responses for any given test face ranges from 0 (i.e., always sad responses to that face) through to 1 (i.e., always happy responses), a value of 0.5 indicates chance performance whereby the participant could not discriminate that test face as either happy or sad (i.e., responses were equally happy and sad). In consistency terms, 0.5 would reflect a consistency percentage score of 0%, indicating greatest uncertainty. By contrast, if a participant responded always happy or always sad, this would indicate perfect consistency and least uncertainty (i.e., 100% consistent with one emotion, thus the proportion of responses is either 1, always happy, or 0, always sad). In this respect, any proportion of happy responses increasingly deviating from 0.5 towards 1, or away from 0.5 towards 0, reflects increasing consistency to happy or sad responses respectively. To calculate the percentage consistency score, we therefore need to make an adjustment that maintains consistency regardless of whether participants are favouring happiness or sadness for any given test face. If the proportion of happy responses to a particular test face was 0.5 or above, we would then subtract 0.5 from this proportion. This would give us a value between 0 through to 0.5, which when multiplied by 200, would range from 0 through to 100; therefore giving us a percentage of how consistently our participants were responding to the face. Conversely, any test face that had a proportion happiness value of less than 0.5, we would then subtract this value

549 from 0.5, and multiply it by 200, thus again giving us a consistency score between 0 to 100%.
550 Any minor differences between how individual participants judge any given test face happy or
551 sad are, therefore, remodelled to reflect their response consistency regardless of emotion. The
552 consistency scores are displayed in Figure 5a, with the controls appearing to be more consistent
553 than the DP cases, at least in judging the happiest test faces. As we found no significant effects
554 for Identity in our prior analyses, we averaged the results of the two adaptor identities together.

555 We performed a $2 \times 3 \times 7$ mixed model ANOVA employing within participant factors of
556 Test Face (0.3, 0.35, 0.4, 0.45, 0.5, 0.55, 0.6) and Adaptor (neutral, happy, hybrid) and a between
557 participant factor of Group (controls vs. DP) in the neutral adaptor condition. We found a
558 significant effect for Group [$F(1,18) = 4.86, p = .041, \eta^2 = .21$] due to the DP cases appearing
559 less consistent ($M = 74\%$) in their emotion judgements relative to the controls ($M = 83\%$). We
560 also found a significant effect of Adaptor [$F(2,36) = 4.66, p = .016, \eta^2 = .34$] due to the happy
561 adaptation condition being judged less consistently than the hybrid, but not the neutral,
562 conditions (happy $M = 73\%$ vs. hybrid $M = 82\%$, $p = .024$, Cohen's $d = .26$; neutral $M = 79\%$, p
563 $= .2$, Cohen's $d = .48$). No differences were found between the hybrid and neutral conditions (p
564 $= .024$, Cohen's $d = .64$). There was also a significant main effect for Test Face [$F(6, 108) =$
565 $17.17, p < .001, \eta^2 = .49$]. This was due to the 0.3, 0.35 and 0.6 (proportion of happiness) test
566 faces being judged more consistently than the 0.45 and 0.5 test faces, with the 0.55 face also
567 more consistently judged than the 0.45 face (all $ps < .05$). Participants were also more consistent
568 when judging the 0.35 and 0.6 faces than the 0.4 test face (all $ps < .05$).

569 Interestingly, there was also a significant Test Face \times Group interaction [$F(6,108) = 2.3,$
570 $p = .04, \eta^2 = .11$] due to the controls appearing more consistent in their judgments to the three
571 happiest test faces (Figure 5a: 0.5, Control $M = 81\%$ vs. DP $M = 65\%$, $p = .026$, Cohen's $d = .85$;



572

573 Figure 5. Controls (filled blue, n = 10) and DP cases' (filled white, n = 10) a) consistency
 574 measures and b) response times to the test faces averaged across all adaptors. Error bars indicate
 575 \pm SEM. Between group comparisons are Bonferroni corrected with p values < .1 reported.

576 0.55, Control $M = 92\%$ vs. DP $M = 71\%$, $p = .003$, Cohen's $d = 1.13$; 0.6, Control $M = 93\%$ vs.
577 DP $M = 78\%$, $p = .022$, Cohen's $d = .92$) but not the 4 saddest faces (0.3, Control $M = 91\%$ vs.
578 DP $M = 90\%$, $p = .89$, Cohen's $d = .02$; 0.35, Control $M = 90\%$ vs. DP $M = 89\%$, $p = .78$,
579 Cohen's $d = .12$; 0.4, Control $M = 72\%$ vs. DP $M = 70\%$, $p = .86$, Cohen's $d = .27$; 0.45, Control
580 $M = 64\%$ vs. DP $M = 53\%$, $p = .15$, Cohen's $d = .5$). This indicates a specific impairment in
581 judging facial happiness in DP.

582 There was no significant Group \times Adaptor interaction [$F(2,36) = .07$, $p = .94$, $\eta^2 = .04$].
583 However, there was a marginally non-significant Adaptor \times Test Face \times Group interaction
584 [$F(12,216) = 1.77$, $p = .054$, $\eta^2 = .09$]. To further investigate this interaction, we performed
585 subsidiary 2 \times 7 mixed model ANOVAs with respective factors of Group and Test Face on each
586 adaptation condition. These analyses yielded no significant main effects of Group [neutral,
587 $F(1,18) = 3.95$, $p = .062$, $\eta^2 = .18$; happy, $F(1,18) = 2.74$, $p = .12$, $\eta^2 = .13$; hybrid, $F(1,18) =$
588 3.15 , $p = .093$, $\eta^2 = .15$]. While all conditions did exhibit a significant main effect for Test Face
589 [neutral, $F(6,108) = 9.96$, $p < .001$, $\eta^2 = .36$; happy, $F(6,108) = 8.06$, $p < .001$, $\eta^2 = .31$; hybrid,
590 $F(6,108) = 10.92$, $p < .001$, $\eta^2 = .38$], the causes of such effects are not of interest as we are only
591 concerned with any between group differences, thus we do not report their subsidiary
592 comparisons. More importantly, there were significant Group \times Test Face interactions in the
593 neutral [$F(6,114) = 2.22$, $p = .046$, $\eta^2 = .17$] and hybrid [$F(6,114) = 2.35$, $p = .035$, $\eta^2 = .11$], but
594 not the happy [$F(6,114) = .53$, $p = .79$, $\eta^2 = .01$], conditions. Subsidiary comparisons revealed the
595 interaction in the neutral condition was due to reduced consistency scores in the DP cases for the
596 four happiest test faces (all $ps < .05$). In the hybrid condition, the DP cases were only less
597 consistent for the three happiest faces (all $ps < .05$). These results suggest that while DP cases
598 were generally impaired in judging facial happiness, this difference was diminished in the happy

599 adaptation condition presumably due to the controls experiencing greater levels of emotion
600 adaptation, thus driving down their consistency scores. Similarly, our controls' adaptation to the
601 happy information in the hybrid appears to have abolished any consistency differences between
602 the groups when judging the fourth happiest test face, in comparison to the neutral condition.
603 Overall, however, the DP cases exhibited deficits in judging the happiest, but not the saddest,
604 facial expressions.

605 *3.4. Response Times*

606 In addition to consistency, slower response times to the test faces by the DP participants
607 could indicate abnormalities in their ability to detect emotion. As with the consistency analyses,
608 we collapsed the two facial identities together to give us mean response times to each test face as
609 shown in Figure 5b. The same $2 \times 3 \times 7$ ANOVA employed on the consistency scores was used
610 on the response times in each adaptation condition. There was no significant main effect for
611 Adaptor [$F(2,36) = 2.97, p = .064, \eta^2 = .14$] or Group [$F(1,18) = 2.91, p = .11, \eta^2 = .14$], but there
612 was a significant effect for Test Face [$F(6,108) = 6.52, p < .001, \eta^2 = .27$]. This was due to
613 participants being faster when responding to the saddest (0.3) and second happiest (0.55) test
614 faces in comparison to the more ambiguous 0.4 and 0.45 test faces (all $ps < .05$). There was also
615 no significant Adaptor \times Test Face interaction [$F(12,216) = 1.53, p = .12, \eta^2 = .08$].

616 While there were no Group \times Adaptor [$F(2,36) = .33, p = .72, \eta^2 = .02$] or Group \times Test
617 Face \times Adaptor [$F(12,216) = 1.24, p = .26, \eta^2 = .06$] interactions, there was a significant Test
618 Face \times Group interaction [$F(6,108) = 2.62, p = .021, \eta^2 = .13$]. This was due to a trend for the DP
619 cases responding slower to the 3 happiest (Figure 6b: 0.5, Control $M = 727$ ms vs. DP $M = 1199$
620 ms, $p = .031$, Cohen's $d = 1.1$; 0.55, Control $M = 648$ ms vs. DP $M = 935$ ms, $p = .057$, Cohen's
621 $d = .91$; 0.6, Control $M = 611$ ms vs. DP $M = 1085$ ms, $p = .051$, Cohen's $d = .94$), but not

622 saddest (0.3, Control $M = 678$ ms vs. DP $M = 895$ ms, $p = .26$, Cohen's $d = .53$; 0.35, Control M
623 $= 732$ ms vs. DP $M = 894$ ms, $p = .46$, Cohen's $d = .34$; 0.4, Control $M = 835$ ms vs. DP $M =$
624 1117 ms, $p = .13$, Cohen's $d = .72$; 0.45, Control $M = 943$ ms vs. DP $M = 1127$ ms, $p = .28$,
625 Cohen's $d = .5$), test faces. Overall, this trend seems to support our hypothesis that DP cases
626 exhibit a specific impairment at judging happy facial expressions.

627

628 **4. Discussion**

629 *Summary of main findings*

630 We presented an argument in the introduction that the processing of facial happiness and
631 identity were not entirely dissociable. In the present study, we set out to test this hypothesis by
632 examining whether individuals with DP could process happy facial expressions with or without
633 awareness. We anticipated that if happiness perception relied upon the same network as facial
634 identity, then those with DP should present comorbid difficulties in perceiving happiness as well
635 as their deficits in identity recognition. While our controls exhibited adaptation aftereffects to the
636 happy and hybrid faces, our DP cases only produced aftereffects, albeit of a smaller magnitude,
637 to the intact happy faces. In addition to impaired adaptation to facial happiness, DP cases were
638 impaired in their response consistency at judging the happiest, but not the saddest, test faces.
639 Finally, this pattern of impairment for the happiest faces also seemed apparent in our DP cases'
640 delayed response times. Overall, our findings seem to fit with the hypothesis that the perception
641 of facial happiness is reliant upon the facial identity recognition network.

642

643

644 *Perception and recognition of facial happiness is impaired in DP*

645 Our DP cases exhibited smaller adaptation aftereffects in comparison to our controls after
646 adapting to the intact happy face adaptors. Curiously, it is noticeable that the magnitude of this
647 difference was similar to the difference between the controls and DP cases' hybrid condition; the
648 latter of whom had a complete absence of any significant aftereffects in their hybrid condition.
649 We interpret this similar decrease in adaptation in the happy and hybrid conditions in our DP
650 cases as being due to a deficit in detecting the LSF of happy facial expressions (i.e., ≤ 6 cycles).
651 The aftereffects produced by the DP cases in the happy adaptor condition must therefore be due
652 to information conveyed in the other spatial frequencies (i.e., > 6 cycles). It is likely that happy
653 facial expressions in these higher spatial frequencies are processed qualitatively differently from
654 LSF, as shown by our DP cases producing adaptation aftereffects to this information. As LSF are
655 thought to support holistic processing (Collishaw & Hole, 2000; Goffaux et al., 2005; Goffaux &
656 Rossion, 2006), it would appear that those with DP have a deficit in processing happy emotional
657 content from faces in a holistic fashion. Instead, we believe that they must have to rely more
658 strongly upon featural aspects of a face to produce emotion adaptation aftereffects. Our results
659 complement similar adaptation work that has shown DP is also associated with abnormal coding
660 of facial identity (Palermo et al., 2011). Taken together, our findings seem to support the
661 proposal that the processing of facial happiness is integrated within the facial identity recognition
662 network.

663 In addition to impaired adaptation to happy facial expressions, our DP cases also exhibited
664 deficits in explicitly judging facial happiness, both in their response times and consistency. This
665 result is in contrast to previous findings that have shown explicit emotion recognition to be
666 spared in DP (Duchaine et al., 2003; Humphreys et al., 2007; Palermo et al., 2011). Instead, we

667 support recent work in suggesting that DP is associated with emotion recognition impairments
668 (Biotti & Cook, 2016). The lack of impairment to the saddest test faces may suggest that our DP
669 cases are neurotypical in their ability to explicitly judge facial sadness, and that the recognition
670 of sadness and happiness are therefore dissociable. However, it should be stressed that this
671 dissociation was not clearly shown here as we did not test additional morphed faces at the
672 sadness end of the test face continuum. Future work will be required to confirm the suggestion
673 that the recognition of facial sadness, and any other emotion other than happiness, is entirely
674 spared in DP. An additional point worth making is that it has been common for researchers using
675 morph continua stimuli to only examine performance between neuropsychological groups using
676 similar analyses as our slope measure (e.g., Biotti & Cook, 2016; Cook et al., 2013). We have
677 shown here that in addition to slope, it is certainly worthwhile performing further analyses on the
678 response times and consistency scores for any given test face. These results can give interesting
679 insights into which specific emotions neuropsychological populations may be experiencing
680 difficulties with, and should enable researchers to highlight dissociations between the perception
681 of individual emotions and other cognitive functions.

682 It may be the case that DP is characterised by a general difficulty in processing the LSF of
683 faces. One other paper backs up this suggestion, with their DP cases exhibiting a delay of around
684 230ms in the processing of the LSF of facial gender (Awasthi, Friedman, & Williams, 2012).
685 This is perhaps surprising, as DP cases have typically been shown to have intact gender
686 judgments (Chatterjee & Nakayama, 2012; Dobel et al., 2007; Le Grand et al., 2006), but these
687 latter results may have been due to perception being attained through the use of high spatial
688 frequencies alone. In contrast to Awasthi and colleagues' findings, our results seem to indicate
689 that DP cases' neuronal populations have a severe inability in differentiating facial happiness and

690 neutral expressions from their LSF, rather than a simple delay in processing this information. If
691 this information was merely delayed by a couple hundred milliseconds, then we should have
692 seen evidence of neuronal habituation in the form of aftereffects that differentiated the LSF of
693 hybrid and neutral facial expressions; an outcome that was not realised here (Figure 2b). That
694 said, our test faces were only presented onscreen for 200 ms. It is therefore unclear whether our
695 test face presentation time was too short for adaptation to the LSF to manifest themselves in our
696 DP cases' aftereffects. Regardless of this fact, our paradigm has highlighted an impairment in
697 our DP cases' capabilities in processing the LSF of facial happiness either with or without
698 awareness. These findings certainly invite further work to investigate whether the deficits in
699 processing LSF in DP are specifically related to faces, or whether they occur as a more general
700 low level visual impairment regardless of context.

701 *Links between autism and DP?*

702 Our results and those of Awasthi and colleagues, however, at the very least indicate some
703 kind of perceptual impairment in DP cases' abilities at processing the LSF of facial happiness
704 and gender. The hypothesis that impaired face perception in DP is due to a deficit in processing
705 of LSF is corroborated by another neuropsychological group that exhibits deficits in face
706 recognition: those with autism (e.g., Annaz, Karmiloff-Smith, Johnson, & Thomas, 2009;
707 Kirchner, Hatri, Heekeren, & Dziobek, 2011; O'Hearn, Schroer, Minshew, & Luna, 2010;
708 Wallace, Coleman, & Bailey, 2008; for a review, see Weigelt, Koldewyn, & Kanwisher, 2012).
709 Individuals with autism have been shown to exhibit similar abnormalities in the perception of
710 faces' LSF (Deruelle, Rondan, Gepner, & Tardif, 2004; Katsyri, Saalasti, Tiippana, von Wendt,
711 & Sams, 2008). These findings suggest a possible commonality between the impaired perception

712 of facial information in DP and autism, and indicate that these two groups may share more
713 common difficulties than previously thought.

714 One surprising aspect of our results, where DP cases differ from those with autism, is that
715 our cases produced adaptation aftereffects of a smaller magnitude to the intact happy faces in
716 comparison to our controls. Previous work in adults with autism has shown that they can produce
717 comparable emotion adaptation aftereffects to neurotypical individuals (Cook et al., 2014).
718 However, a recent paper has indicated that this seemingly intact emotion adaptation may only
719 arise due to an increased reliance upon perceiving emotion from the mouth as levels of autism
720 increase (Luo et al., 2017). When the mouth region was obscured, increasing autistic traits were
721 associated with decreasing adaptation aftereffects (Luo et al., 2017). As the mouth is important
722 in happiness recognition (Beaudry et al., 2014), those high in autistic traits must have had
723 difficulties in perceiving happiness in a holistic fashion when the mouth was obscured (Luo et
724 al., 2017). The fact that our DP cases were unable to produce neurotypical levels of adaptation to
725 the intact happy faces would seem to indicate possible differences in the way that emotion is
726 perceived in those high in autistic traits and DP.

727 *Implications for awareness and neural locus of happiness perception*

728 As earlier mentioned, our DP cases seem to lack an ability to adapt to the LSF of the happy
729 and hybrid faces, regardless of whether they are aware of this emotional information or not. This
730 result is in contrast to the suggestion that the processing of emotional faces without awareness is
731 qualitatively different from that when processed with awareness (Tamietto & De Gelder, 2010).
732 At least in the case of facial happiness conveyed in the LSF, awareness does not lead to any
733 qualitative differences in how this information drives emotion adaptation. By contrast, happy

734 information in the HSF seems to drive awareness of emotion, most likely due to participants
735 explicitly identifying facial happiness from the visible features of the face. The fact that our DP
736 cases can seemingly adapt to HSF, as shown by their adaptation aftereffects in the happy
737 condition, would suggest a qualitative difference in how the LSF and HSF of happiness are
738 processed in the brain. As the changeable aspects of facial features during emotional expressions
739 are commonly thought to be processed through the STS (Haxby & Gobbini, 2011), it would
740 seem likely that this is the route through which adaptation to facial happiness with awareness
741 arises.

742 What region in the cortical face perception network is causing the diminished adaptation
743 aftereffects and impaired perception happy facial expressions in DP? fMRI research has
744 indicated that the LSF of faces must in some way be processed by the FFA (Rotshtein et al.,
745 2007; Winston et al., 2003). The FFA in DP is associated with reduced grey matter volume
746 (Garrido et al., 2009), diminished differences in neural activity between neutral and happy faces
747 (Van den Stock et al., 2008), and abnormal sensitivity to the holistic configuration of a face
748 (Zhang et al., 2015). DP cases have also been shown to exhibit similarly abnormal holistic
749 coding of emotion and identity (Palermo et al., 2011). As LSF are thought to drive holistic
750 processing (Collishaw & Hole, 2000; Goffaux et al., 2005; Goffaux & Rossion, 2006), it would
751 therefore seem plausible to suggest that the FFA is the most likely candidate for the diminished
752 adaptation aftereffects and impaired recognition of happy facial expressions observed here in
753 DP. The FFA has also been shown by both neuropsychological (Barton, 2008) and neuroimaging
754 (Rotshtein et al., 2005; Schiltz et al., 2006) work to be important in the processing of facial
755 identity and the processing of happy expressions (Tsuchiya et al., 2008). From the above
756 evidence, we propose that the neurotypical processing of facial identity, and happy facial

757 expressions either with or without awareness, share a common neural substrate in the FFA. This
758 hypothesis would require prominent models of face processing that propose facial identity and
759 emotion are dissociable to undergo considerable modification to incorporate this suggestion
760 (Bruce & Young, 1986; Haxby et al., 2000). Instead, our findings seem to support alternative
761 perspectives that posit the processing of identity and emotion, at least in the case of facial
762 happiness, are reliant upon shared processes (Calder, 2011; Rhodes et al., 2015).

763 The bulk of prior neuroimaging studies examining how the brain processes LSF have
764 primarily focused on fearful faces (De Jong et al., 2008; Holmes et al., 2005; Morawetz et al.,
765 2011; Vuilleumier et al., 2004; Winston et al., 2003). Many studies examining emotion
766 processing fail to consider the qualitatively different ways in which other facial emotions' LSF
767 may be processed. Laeng et al (2010) found that while amygdala damage led to deficits in the
768 implicit processing of emotional content conveyed by the LSF of sad and fearful faces, the
769 processing of angry and happy LSF remained spared. This suggests that the cortical route is
770 possibly required to detect the LSF of angry and happy faces, with the amygdala processing the
771 LSF of sad and fearful faces. We suggest that further neuroimaging research will confirm the
772 functional role of the FFA in processing the LSF of angry and happy facial expressions, but not
773 those of sadness or fear.

774 *Constraints and limitations*

775 One limitation of our study that we must accept is that all, or at least a considerable
776 number, of our DP cases may have been impaired in their ability to recognise emotion. Such
777 cases with severe deficits in emotion recognition are apparent in the literature (for a recent
778 summary, see Biotti and Cook, 2016), and the lack of an alternative emotion recognition task

779 makes us unable to ascertain the extent to which this may be driving our results. Biotti and
780 Cook's (2016) work suggests that those DP cases that have face perception issues, as opposed to
781 solely face memory difficulties, are more likely to suffer from concurrent emotion perception
782 problems. However, our 2 apperceptive DP cases, as shown by the CFPT, were likely
783 insufficient to drive the group deficits observed here. Instead, it seems that DP cases as a group,
784 regardless of whether they have perceptual problems too, do seem to have deficits in the
785 recognition of facial happiness. As mentioned earlier though, it is difficult to ascertain how valid
786 the CFPT is in identifying perceptual deficits in non-Caucasian populations, so the extent to
787 which we can make such assumptions needs to be severely constrained.

788 It should be noted that our results could also have a surprising alternative interpretation.
789 In our initial analyses on the raw PSE values, we find that our DP cases only significantly differ
790 from the controls in the intact neutral adaptation condition. Similarly, we only find significant
791 slope differences between our two groups in their neutral face condition. This may suggest that
792 our DP cases are only abnormal when adapting to the neutral faces, and may adapt to the hybrid
793 and happy faces in a neurotypical manner due to comparable PSE and slope values between the
794 two groups. We, however, do not believe that this is the case. First, our consistency measures
795 and response times to the happiest test faces seem to indicate that DP is associated with a
796 specific impairment in detecting facial happiness. Second, our DP cases may have adapted to the
797 neutral face's expression in a neurotypical way (i.e., no adaptation), it is just that they only
798 exhibit this PSE shift because their neural signal of happiness from the test faces is degraded due
799 to abnormalities in their cortical face perception areas. The sadness signal from the amygdala,
800 which is presumably intact in DP (Behrmann et al., 2007; Dinkelacker et al., 2010; Van den
801 Stock et al., 2008), would thus have a stronger influence on our DP cases' judgments of emotion

802 to the test faces. The resulting PSE shift could be explained due to this sadness signal not being
803 counteracted by the perception of happiness from the cortical route in DP, rather than any
804 differential effects of adaption to the neutral face *per se*. If this were the case, then it can explain
805 why our DP cases were no different in their PSE values, consistency judgements and response
806 times between the neutral and hybrid conditions: it is due to a common inability at being able to
807 adapt to the LSF of the hybrid and neutral adaptors. While unpublished data by our lab indicates
808 that no adaptation results in the same PSE and slope values as a neutral face adaptation condition
809 in neurotypical individuals, it is as present unknown whether this holds true for DP cases. Future
810 adaptation work should, therefore, take the cautionary measure of including a no adaptation
811 baseline condition. This would give a pure PSE value from the test faces alone and allow
812 researchers to confirm the suggestion that DP cases are adapting to the neutral face in a
813 neurotypical way (i.e., no adaptation).

814 We had not considered the possibility that changing facial identity between the adaptation
815 and test faces may have led to a greater level of disruption in our DP cases' aftereffects in
816 comparison to our controls. One may imagine that when our controls noticed the switching facial
817 identities between the adaptation and test periods, it led to an increase in attention that resulted in
818 greater adaptation aftereffects (Ewing, Leach, Pellicano, Jeffery, & Rhodes, 2013). This would
819 be in contrast to our DP cases who, by possibly not noticing this change in identity, would not
820 receive this attention related boost in their aftereffects. This hypothesis, however, does not seem
821 to hold up to scrutiny, as matched identities between adaptor and test typically result in larger
822 aftereffects (Fox & Barton, 2007). Thus, we would surely expect our DP cases to produce larger
823 aftereffects due to their greater likelihood of appraising both the adaptors and test faces as being
824 the same identity. This possibility, therefore, makes the reduction in adaptation aftereffects in our

825 DP cases all the more remarkable. While confirming this suggestion is beyond the scope of the
826 present study, future work should answer whether DP cases' aftereffects are similarly boosted by
827 attention or the recognition of matching facial identities between adaptation and test.

828 *Conclusions*

829 We have shown that DP is associated with deficits in the adaptation to, and recognition of,
830 happy facial expressions. These abnormalities in emotion adaptation are consistent regardless of
831 the DP cases' awareness of the emotion they are viewing. We hypothesise that these deficits are
832 due to previously identified abnormalities in the FFA's grey matter density and neural
833 functioning in DP. This is in contrast to the suggestion that emotion processing without
834 awareness can occur through subcortical structures without input from the FFA. In addition,
835 models of face recognition have typically proposed that emotion recognition is attained through
836 neural structures that are functionally distinct from those that process identity. Despite previous
837 DP research appearing to confirm this suggestion, we have shown that due to associated deficits
838 in DP, the recognition of happy facial expressions is likely to be identified through similar
839 structures as those used to recognise facial identity. While we focused on the processing of
840 happy, and to a lesser extent sad, facial emotions, the hint of a dissociation observed here
841 suggests that future researchers should carefully examine performance of individual emotions
842 when testing neuropsychological populations. Such work will help further clarify overlapping,
843 and dissociable, cognitive processes in identity and emotion recognition.

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854

855 **6. Author Contributions**

856 E. B. and H. X. designed the experiment. E. B. collected and analysed the data. J. M. created
857 the adapting stimuli. E. B. and H. X. wrote the manuscript with the other authors responsible for
858 manuscript review and comments.

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