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Edwin Burns
University of Richmond
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Impaired processing of facial happiness, with or without awareness, in developmental prosopagnosia

Edwin J. Burns[1], Joel Martin[2], Alice H.D. Chan[3] & Hong Xu[1]

[1]Division of Psychology, School of Social Sciences, Nanyang Technological University

[2]Department of Psychology, Swansea University

[3]Linguistics and Multilingual Studies, School of Humanities, Nanyang Technological University

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*Correspondence: Dr. Hong Xu
14 Nanyang Drive, HSS-04-06
Division of Psychology
School of Social Sciences
Nanyang Technological University
Singapore 637332
Phone: +65 6592-1571
Fax: +65 6795-5797
Email: xuhong@ntu.edu.sg

Abstract

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

Abstract word count: 255 words.

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

Highlights

Processing of facial happiness is impaired in developmental prosopagnosia

These impairments persist when processing should occur without awareness

Our cases also exhibited deficits in explicitly judging happy expressions

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

1. Introduction

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

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

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

Direct evidence that facial happiness is processed through the FFA comes from neuroimaging and neuropsychological research. Tsuchiya and colleagues (2008) found that activity in the ventral temporal cortex (which includes the FFA) was associated with the discrimination of facial happiness over fear. Differential neural responses have also been apparent in the FFA of neurotypical individuals viewing happy versus neutral facial expressions (Van den Stock et al., 2008). In the same study, developmental prosopagnosia (DP) cases, individuals who suffer from lifelong impairments in face recognition, had a reduction in their FFA's differential neural activity when viewing these two different facial expressions. These findings not only indicate that the FFA is partly specialised for the processing of facial happiness, but that its ability in DP to distinguish neutral from happy facial expressions might be compromised.

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

Remarkably, no study to date has shown that DP cases are impaired in their perception of facial happiness or abnormal in their processing of emotion without conscious awareness. The processing of facial emotion without awareness is thought to occur in a qualitatively different way, that is through the amygdala, in contrast to when it is processed with awareness through the cortex (Tamietto & De Gelder, 2010). DP cases have been shown to exhibit amygdala that are typically intact both structurally and in their functioning (Behrmann et al., 2007; Dinkelacker et al., 2010; Van den Stock et al., 2008). If the processing of facial emotion without awareness occurs through this subcortical route as is commonly argued (Tamietto & De Gelder, 2010), then we should expect those with DP to be unimpaired when attempting to process such information. By contrast, if facial happiness were to traverse a cortical route which includes the FFA, then those with DP will likely exhibit impairments in perceiving happy facial expressions.

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

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

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

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

2. Methods

2.1. Participants

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

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

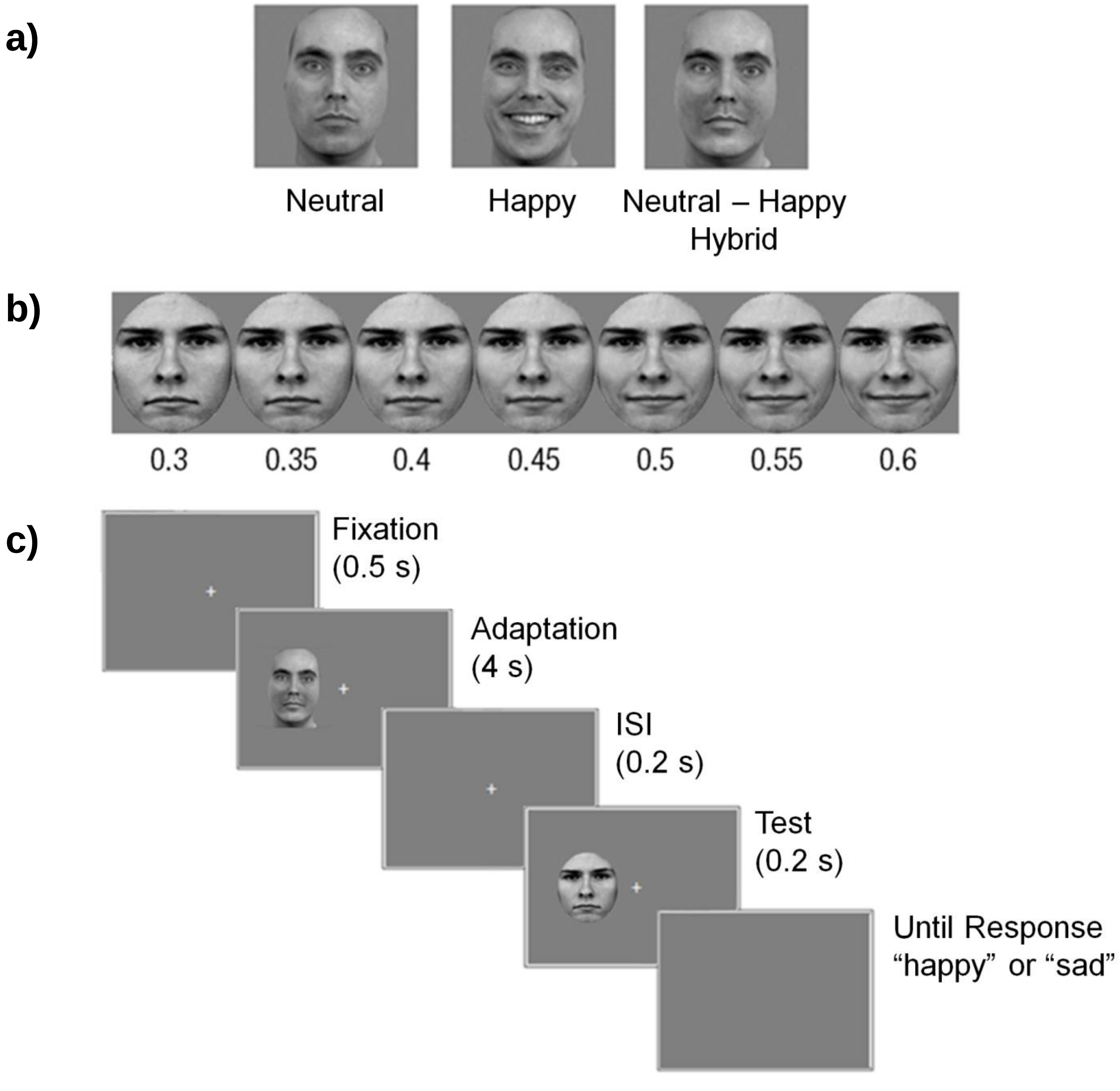

Figure 1. Examples of Stimuli and Trial Sequence. a) Three different adapting stimuli for one of the two identities (from left to right): intact neutral face, intact happy face, and the neutral-happy hybrid face. b) Test faces ranging in proportion of happiness from 0.3 through to 0.6. c) Example of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

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

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

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

During the Cambridge Face Perception Test (CFPT; Duchaine et al., 2007), participants are shown a target face presented in three-quarter view along with 6 faces presented in frontal view; these 6 faces have been morphed to appear similar in varying percentages to the target face. Participants are required to arrange the faces in order of similarity to the target face. The test displays faces either upright or inverted. As there is no Chinese version available for this test, we collected normative scores from a local Chinese sample (*N* = 12) to see whether performance on this task can be comparable regardless of ethnicity. Remarkably, the Chinese scores on the upright (*M* = 32.2, *SD* = 11.6) and inverted (*M* = 62.3, *SD* = 12.8) portions of this task were almost identical to previous studies of Caucasians (Bowles et al., 2009; Duchaine, Germine et al., 2007; Garrido et al., 2008). To our knowledge, this is the first time that the CFPT has been shown to be comparable between the neurotypical Caucasian and Chinese populations. This is in contrast to the CFMT which elicits stark differences across Chinese and Caucasian populations (McKone et al., 2012), with both experiencing the other race effect; that is, better performance for their own race (Chiroro et al., 2008).

It may initially seem that these results confirm the CFPT's validity in detecting face perception deficits in ethnic Chinese. However, it may be possible that our neurotypical Chinese participants were using domain general perceptual processes (Furl, Garrido, Dolan, Driver, & Duchaine, 2011) that are in some way distinct from the face-related processes employed by their Caucasian counterparts. Support for this point comes from the lack of an other race effect, that is, poorer performance in our Chinese participants when processing Caucasian faces on the CFPT in comparison to Caucasians in the literature (Bowles et al., 2009; Duchaine, Germine et al., 2007; Garrido et al., 2008). This argument, however, does seem countered by the fact that our Chinese participants exhibited an inversion effect (Yin, 1969), that is, better performance when faces are presented upright versus inverted: a classic index of face-related processing (Valentine, 1988). If our participants were using domain general processes on this task, then we would expect to see little difference between upright and inverted performance; an outcome that was not realised here. While our Chinese participants do not seem worse than Caucasians on the CFPT, the lack of a Chinese version of this task makes it difficult to confirm whether our Chinese cases would exhibit an other race effect on the CFPT. Thus, any interpretation of this data should be taken with caution. The creation of a Chinese CFPT, however, would certainly be beneficial for diagnosing apperceptive prosopagnosia cases in ethnic Chinese. Table 1 shows that only two cases were abnormal on the CFPT. Keeping in line with previous DP research (Bate et al., 2014; Burns et al., 2014), however, our criteria for identifying DP cases required impairment on both the CFMT and FFT.

2.2. Stimuli

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

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

The stimuli were presented on a 15.6” computer monitor screen, to the left of a fixation cross as shown in Figure 1, with a center-to-center distance of 4.3°. The computer screen was approximately 60cm from the participant’s face, with the adapting stimuli subtending horizontal and vertical visual angles of 3.8° and 5.7° respectively. The test face stimuli subtended horizontal and vertical visual angles of 4.5° and 5.2° respectively. Despite our adaptor and test faces covering roughly the same area on the screen, the unmasked test faces were actually larger than the adapting faces. This incongruence in actual face size between the test and study faces has been used in other adaptation paradigms to reduce retinotopic adaptation (Burton et al., 2015; Rhodes et al., 2015). The vertical refresh rate was 60 Hz, and the spatial resolution was 1366 × 768 pixels. All face stimuli were presented against a grey background. The whole experiment was run using E-Prime 2.0.

2.3. Procedure

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

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

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

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

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

2.4 Data Analysis

To measure emotion adaptation aftereffects, we first calculated the proportion of happy responses for every test face in each adaptation condition. The proportions of happy responses were then plotted against the morphed proportions of happiness in the test faces. The results were then fitted with a sigmoidal function in the form of $f(x) = 1/[1+e^{-a(x-b)}]$, where *b* equals to the 50% point of the psychometric function [the point of subjective equity (PSE)] indicating chance performance, and *a/4* determines the slope and indicates the response sensitivity. As PSE values reflect the point at which perception of emotion becomes uncertain in any particular condition for each participant, they can therefore be used to test differences between comparable levels of perception across conditions and groups. These comparisons can only be made so long as a certain level of accuracy is achieved in order to fit a reliable psychometric curve on the data, something that was possible with all of our participants' results. However, while the PSE calculation is reliant upon a certain level of accuracy, they can still compare the points at which perception performance is matched between two different groups, even if the groups differ in their general judgment consistency as indicated by the slopes of their curves. Similar studies have used PSE values as a reliable index to compare neurotypical and neuropsychological populations (Cook, Brewer, Shah, & Bird, 2013; 2014). The magnitude of the aftereffect was calculated by subtracting the PSE of the baseline (neutral face adaptation) from the adaptation condition(s) of interest. We conducted mixed models Analysis of Variance (ANOVA) to compare different conditions, and then used two-tailed independent samples *t*-tests (with Bonferroni corrections) to follow up on any significant interactions. All analyses were performed in Matlab or SPSS.

3. Results

3.1. Point of Subjective Equality

To quantify and compare the perception of the adaptors' emotions, we calculated the point of subjective equality (PSE: the proportion of happiness in test stimuli that corresponds to 50% happy responses) from the participants' psychometric curves (details in *Data Analysis* section). The average judgements made by all control and DP participants to the test faces after adaptation to the neutral, happy and hybrid adaptors are shown in Figure 2. The controls' psychometric curves after adapting to the neutral, intact happy and hybrid faces seem to differ in PSE. Larger PSE values suggest participants require a greater proportion of facial happiness in the test faces before they can judge a face as happy. The shift between the curves of the intact happy and hybrid face adaptation from the neutral face condition indicates an adaptation aftereffect (more details in the *Emotion adaptation aftereffects* section). In comparison, the differences between these curves for the DP cases are smaller than the controls. The main difference between the two participant groups is in the psychometric curve of the neutral face adaptation. For example, for the same test face near the 0.45 proportion of happiness, the controls judged it as a happy face (black circle in Figure 2a), but the DP cases judged it as a sad face (black circle in Figure 2b). This suggests that the DP cases have a higher threshold for judging the test faces as being happy. Such differences do not seem so apparent between the DP cases and controls in the happy and hybrid conditions.

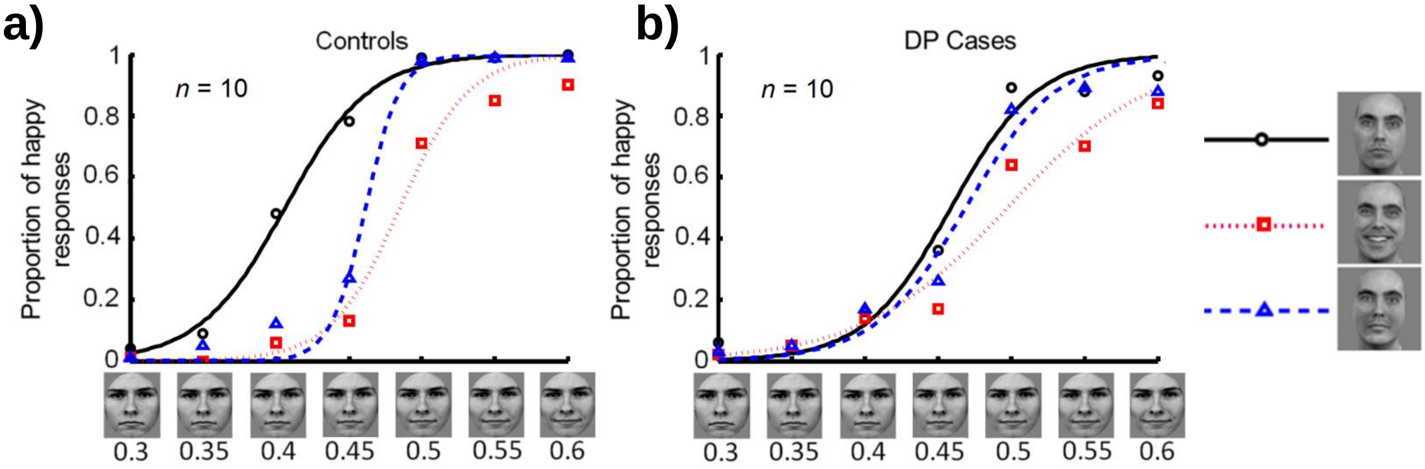

Figure 2. Mean psychometric functions to adaptation from a) neurotypical control participants (left panel) and b) DP cases (right panel). Black lines = neutral face adaptation, red dotted lines = intact happy face adaptation, blue dashed lines = hybrid face adaptation.

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

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

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

3.2. Emotion adaptation aftereffects

Facial emotion aftereffects were calculated by subtracting the PSE of the neutral face conditions from the happy or hybrid conditions. These aftereffect magnitudes would allow us to compare differences in adaptation aftereffects between the two groups. As we previously found no significant effects or interactions involving Identity between the groups, we averaged the PSE values of both identities together. Figure 3 shows the magnitudes of these aftereffects, with larger values reflecting greater emotion adaptation relative to the baseline neutral condition. To compare the magnitudes of these aftereffects between the groups, we performed a 2 × 2 mixed model ANOVA employing a within participant factor of Adaptor (happy vs. hybrid), and a between participant factor of Group (controls vs. DP). We found a significant main effect of Adaptor [$F(1,18) = 25.93$, $p < .001$, $\eta^2 = .59$], indicating that both groups exhibited larger

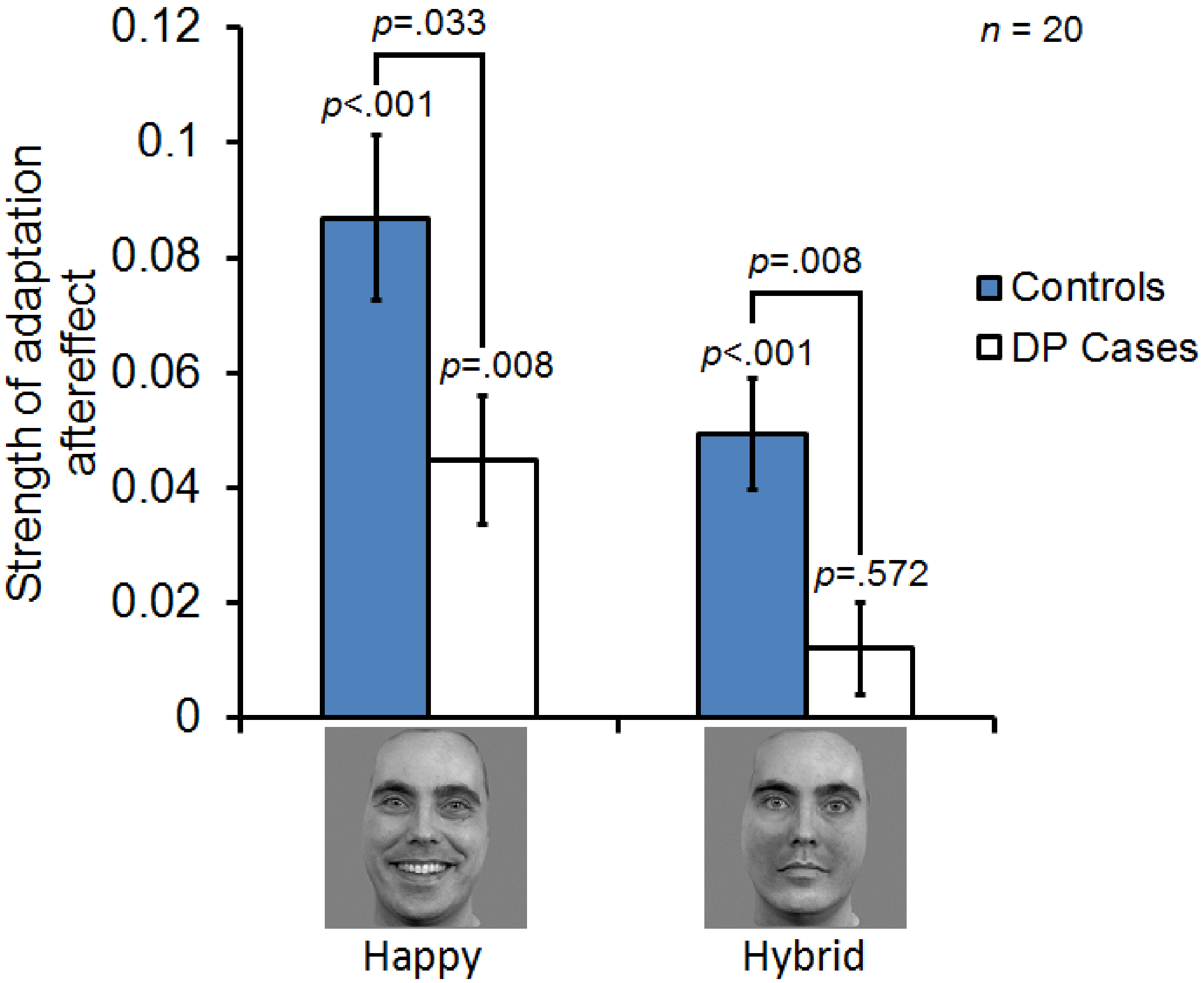

Figure 3. The magnitudes of the emotion adaptation aftereffects for both the controls (filled blue, n = 10) and DP cases (filled white, n = 10). The bars on the left represent the aftereffects to the happy face with the bars on the right showing the aftereffects to the hybrid faces. Comparisons for each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

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

3.2. Sensitivity to emotion in the test faces

To comprehensively examine any emotion sensitivity deficits in DP to the test faces, we calculated the slope values of the psychometric curves for each adaptor (details in our *Data Analysis* section). Our slope values index our participants' general sensitivity at discriminating the two emotions (Liu, Montaser-Kouhsari, Xu, 2014), which is a similar way of examining emotion recognition performance as found in Biotti and Cook's (2016) study. As can be seen from Figure 2, the control participants' slopes for all adaptors appear steeper than the DP cases' slopes. Our calculated slope values are presented in Figure 4, with larger values indicating steeper slopes and better sensitivity at judging the emotions of the test faces. We performed a 2 × 3 mixed model ANOVA on the slope values, with a within subject factor of Adaptor (neutral, happy, hybrid) and a between subject factor of Group (controls vs. DP). There was a close to significant effect with a medium to large effect size for Group [*F*(1,18) = 4.41, *p* = .05, η^2 = .2] due to the controls' psychometric curve slopes ($M = 1.51$) in Figure 2 being steeper in contrast to the DP cases ($M = .85$), suggesting that the controls may be more sensitive in emotion judgment. However, no significant effect [$F(2,36) = .94$, $p = .4$, $\eta^2 = .1$] or interaction [$F(2,36) = .023$, $p = .98$, $\eta^2 = .003$] involving Adaptor was found.

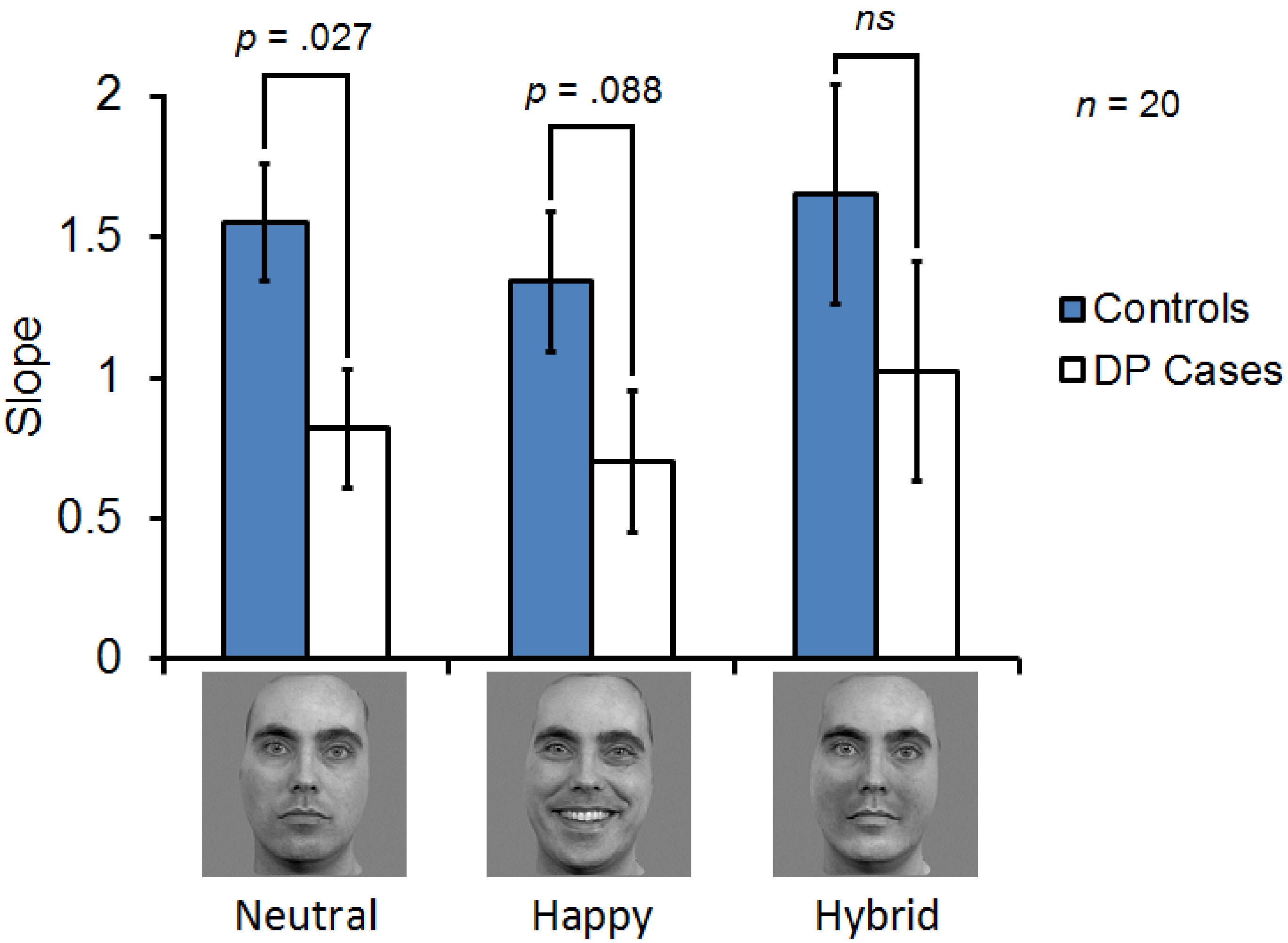

Figure 4. The slope values for controls (filled blue, n = 10) and DP cases (filled white, n = 10). The bars on the left represent the slope after adapting to the neutral face, the bars in the middle the happy face, and the bars on the right the hybrid faces. Larger values suggest better sensitivity at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

3.3. Consistency in judgments of emotion

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

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

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

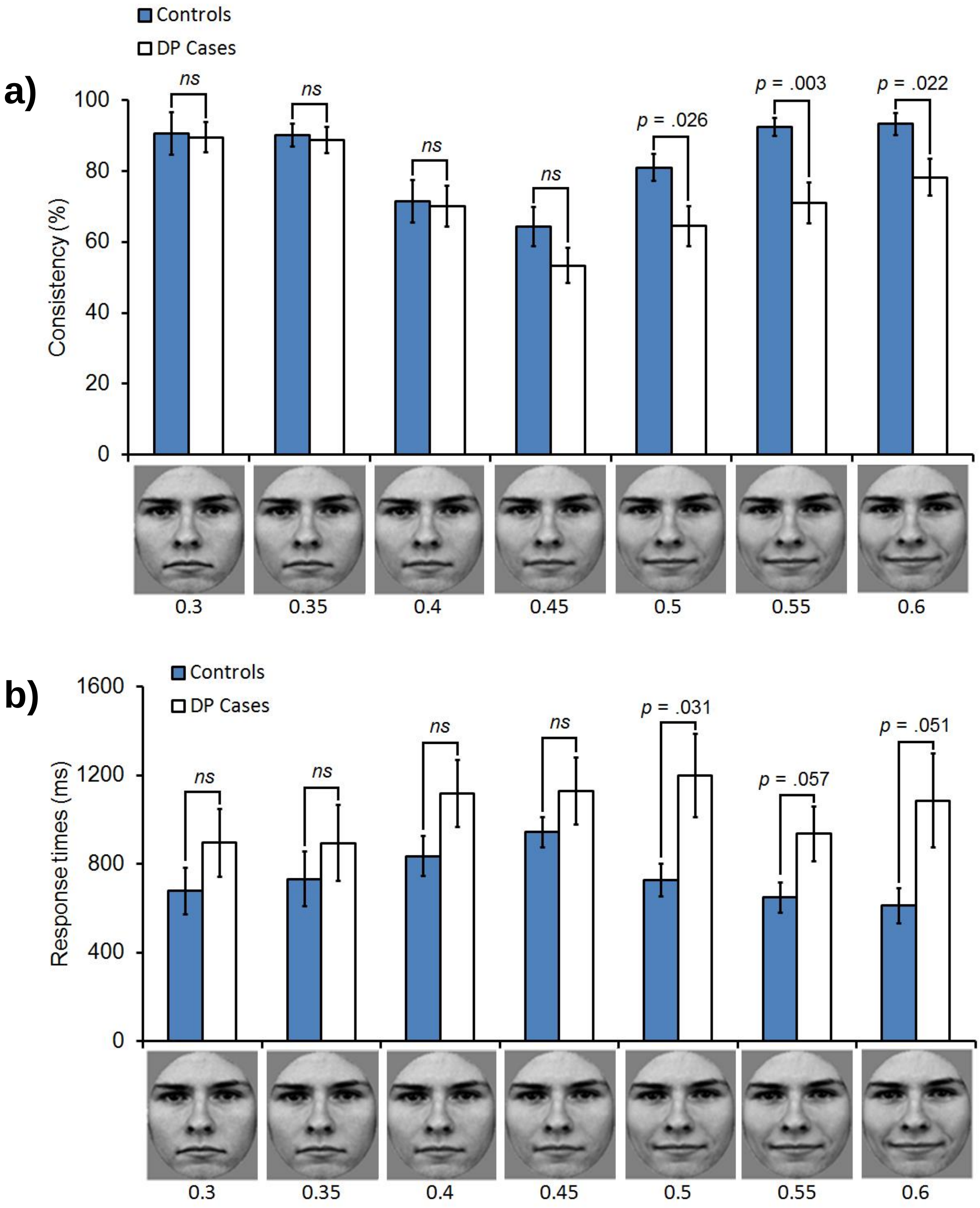

Figure 5. Controls (filled blue, n = 10) and DP cases' (filled white, n = 10) a) consistency measures and b) response times to the test faces averaged across all adaptors. Error bars indicate ±SEM. Between group comparisons are Bonferroni corrected with p values < .1 reported.

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

There was no significant Group × Adaptor interaction [F(2,36) = .07, p = .94, η^2 = .04]. However, there was a marginally non-significant Adaptor × Test Face × Group interaction [F(12,216) = 1.77, p = .054, η^2 = .09]. To further investigate this interaction, we performed subsidiary 2 x 7 mixed model ANOVAs with respective factors of Group and Test Face on each adaptation condition. These analyses yielded no significant main effects of Group [neutral, F(1,18) = 3.95, p = .062, η^2 = .18; happy, F(1,18) = 2.74, p = .12, η^2 = .13; hybrid, F(1,18) = 3.15, p = .093, η^2 = .15]. While all conditions did exhibit a significant main effect for Test Face [neutral, F(6,108) = 9.96, p < .001, η^2 = .36; happy, F(6,108) = 8.06, p < .001, η^2 = .31; hybrid, F(6,108) = 10.92, p < .001, η^2 = .38], the causes of such effects are not of interest as we are only concerned with any between group differences, thus we do not report their subsidiary comparisons. More importantly, there were significant Group × Test Face interactions in the neutral [F(6,114) = 2.22, p = .046, η^2 = .17] and hybrid [F(6,114) = 2.35, p = .035, η^2 = .11], but not the happy [F(6,114) = .53, p = .79, η^2 = .01], conditions. Subsidiary comparisons revealed the interaction in the neutral condition was due to reduced consistency scores in the DP cases for the four happiest test faces (all ps < .05). In the hybrid condition, the DP cases were only less consistent for the three happiest faces (all ps < .05). These results suggest that while DP cases were generally impaired in judging facial happiness, this difference was diminished in the happy adaptation condition presumably due to the controls experiencing greater levels of emotion adaptation, thus driving down their consistency scores. Similarly, our controls' adaptation to the happy information in the hybrid appears to have abolished any consistency differences between the groups when judging the fourth happiest test face, in comparison to the neutral condition. Overall, however, the DP cases exhibited deficits in judging the happiest, but not the saddest, facial expressions.

3.4. Response Times

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

While there were no Group × Adaptor [$F(2,36) = .33$, $p = .72$, $\eta^2 = .02$] or Group × Test Face × Adaptor [$F(12,216) = 1.24$, $p = .26$, $\eta^2 = .06$] interactions, there was a significant Test Face × Group interaction [$F(6,108) = 2.62$, $p = .021$, $\eta^2 = .13$]. This was due to a trend for the DP cases responding slower to the 3 happiest (Figure 6b: 0.5, Control *M* = 727 ms vs. DP *M* = 1199 ms, p = .031, Cohen's *d* = 1.1; 0.55, Control *M* = 648 ms vs. DP *M* = 935 ms, p = .057, Cohen's *d* = .91; 0.6, Control *M* = 611 ms vs. DP *M* = 1085 ms, p = .051, Cohen's *d* = .94), but not saddest (0.3, Control *M* = 678 ms vs. DP *M* = 895 ms, p = .26, Cohen's *d* = .53; 0.35, Control *M* = 732 ms vs. DP *M* = 894 ms, p = .46, Cohen's *d* = .34; 0.4, Control *M* = 835 ms vs. DP *M* = 1117 ms, p = .13, Cohen's *d* = .72; 0.45, Control *M* = 943 ms vs. DP *M* = 1127 ms, p = .28, Cohen's *d* = .5), test faces. Overall, this trend seems to support our hypothesis that DP cases exhibit a specific impairment at judging happy facial expressions.

4. Discussion

Summary of main findings

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

Perception and recognition of facial happiness is impaired in DP

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

In addition to impaired adaptation to happy facial expressions, our DP cases also exhibited deficits in explicitly judging facial happiness, both in their response times and consistency. This result is in contrast to previous findings that have shown explicit emotion recognition to be spared in DP (Duchaine et al., 2003; Humphreys et al., 2007; Palermo et al., 2011). Instead, we support recent work in suggesting that DP is associated with emotion recognition impairments (Biotti & Cook, 2016). The lack of impairment to the saddest test faces may suggest that our DP cases are neurotypical in their ability to explicitly judge facial sadness, and that the recognition of sadness and happiness are therefore dissociable. However, it should be stressed that this dissociation was not clearly shown here as we did not test additional morphed faces at the sadness end of the test face continuum. Future work will be required to confirm the suggestion that the recognition of facial sadness, and any other emotion other than happiness, is entirely spared in DP. An additional point worth making is that it has been common for researchers using morph continua stimuli to only examine performance between neuropsychological groups using similar analyses as our slope measure (e.g., Biotti & Cook, 2016; Cook et al., 2013). We have shown here that in addition to slope, it is certainly worthwhile performing further analyses on the response times and consistency scores for any given test face. These results can give interesting insights into which specific emotions neuropsychological populations may be experiencing difficulties with, and should enable researchers to highlight dissociations between the perception of individual emotions and other cognitive functions.

It may be the case that DP is characterised by a general difficulty in processing the LSF of faces. One other paper backs up this suggestion, with their DP cases exhibiting a delay of around 230ms in the processing of the LSF of facial gender (Awasthi, Friedman, & Williams, 2012). This is perhaps surprising, as DP cases have typically been shown to have intact gender judgments (Chatterjee & Nakayama, 2012; Dobel et al., 2007; Le Grand et al., 2006), but these latter results may have been due to perception being attained through the use of high spatial frequencies alone. In contrast to Awasthi and colleagues' findings, our results seem to indicate that DP cases' neuronal populations have a severe inability in differentiating facial happiness and neutral expressions from their LSF, rather than a simple delay in processing this information. If this information was merely delayed by a couple hundred milliseconds, then we should have seen evidence of neuronal habituation in the form of aftereffects that differentiated the LSF of hybrid and neutral facial expressions; an outcome that was not realised here (Figure 2b). That said, our test faces were only presented onscreen for 200 ms. It is therefore unclear whether our test face presentation time was too short for adaptation to the LSF to manifest themselves in our DP cases' aftereffects. Regardless of this fact, our paradigm has highlighted an impairment in our DP cases' capabilities in processing the LSF of facial happiness either with or without awareness. These findings certainly invite further work to investigate whether the deficits in processing LSF in DP are specifically related to faces, or whether they occur as a more general low level visual impairment regardless of context.

Links between autism and DP?

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

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

Implications for awareness and neural locus of happiness perception

As earlier mentioned, our DP cases seem to lack an ability to adapt to the LSF of the happy and hybrid faces, regardless of whether they are aware of this emotional information or not. This result is in contrast to the suggestion that the processing of emotional faces without awareness is qualitatively different from that when processed with awareness (Tamietto & De Gelder, 2010). At least in the case of facial happiness conveyed in the LSF, awareness does not lead to any qualitative differences in how this information drives emotion adaptation. By contrast, happy information in the HSF seems to drive awareness of emotion, most likely due to participants explicitly identifying facial happiness from the visible features of the face. The fact that our DP cases can seemingly adapt to HSF, as shown by their adaptation aftereffects in the happy condition, would suggest a qualitative difference in how the LSF and HSF of happiness are processed in the brain. As the changeable aspects of facial features during emotional expressions are commonly thought to be processed through the STS (Haxby & Gobbini, 2011), it would seem likely that this is the route through which adaptation to facial happpiness with awareness arises.

What region in the cortical face perception network is causing the diminished adaptation aftereffects and impaired perception happy facial expressions in DP? fMRI research has indicated that the LSF of faces must in some way be processed by the FFA (Rotshtein et al., 2007; Winston et al., 2003). The FFA in DP is associated with reduced grey matter volume (Garrido et al., 2009), diminished differences in neural activity between neutral and happy faces (Van den Stock et al., 2008), and abnormal sensitivity to the holistic configuration of a face (Zhang et al., 2015). DP cases have also been shown to exhibit similarly abnormal holistic coding of emotion and identity (Palermo et al., 2011). As LSF are thought to drive holistic processing (Collishaw & Hole, 2000; Goffaux et al., 2005; Goffaux & Rossion, 2006), it would therefore seem plausible to suggest that the FFA is the most likely candidate for the diminished adaptation aftereffects and impaired recognition of happy facial expressions observed here in DP. The FFA has also been shown by both neuropsychological (Barton, 2008) and neuroimaging (Rotshtein et al., 2005; Schiltz et al., 2006) work to be important in the processing of facial identity and the processing of happy expressions (Tsuchiya et al., 2008). From the above evidence, we propose that the neurotypical processing of facial identity, and happy facial expressions either with or without awareness, share a common neural substrate in the FFA. This hypothesis would require prominent models of face processing that propose facial identity and emotion are dissociable to undergo considerable modification to incorporate this suggestion (Bruce & Young, 1986; Haxby et al., 2000). Instead, our findings seem to support alternative perspectives that posit the processing of identity and emotion, at least in the case of facial happiness, are reliant upon shared processes (Calder, 2011; Rhodes et al., 2015).

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

Constraints and limitations

One limitation of our study that we must accept is that all, or at least a considerable number, of our DP cases may have been impaired in their ability to recognise emotion. Such cases with severe deficits in emotion recognition are apparent in the literature (for a recent summary, see Biotti and Cook, 2016), and the lack of an alternative emotion recognition task makes us unable to ascertain the extent to which this may be driving our results. Biotti and Cook's (2016) work suggests that those DP cases that have face perception issues, as opposed to solely face memory difficulties, are more likely to suffer from concurrent emotion perception problems. However, our 2 apperceptive DP cases, as shown by the CFPT, were likely insufficient to drive the group deficits observed here. Instead, it seems that DP cases as a group, regardless of whether they have perceptual problems too, do seem to have deficits in the recognition of facial happiness. As mentioned earlier though, it is difficult to ascertain how valid the CFPT is in identifying perceptual deficits in non-Caucasian populations, so the extent to which we can make such assumptions needs to be severely constrained.

It should be noted that our results could also have a surprising alternative interpretation. In our initial analyses on the raw PSE values, we find that our DP cases only significantly differ from the controls in the intact neutral adaptation condition. Similarly, we only find significant slope differences between our two groups in their neutral face condition. This may suggest that our DP cases are only abnormal when adapting to the neutral faces, and may adapt to the hybrid and happy faces in a neurotypical manner due to comparable PSE and slope values between the two groups. We, however, do not believe that this is the case. First, our consistency measures and response times to the happiest test faces seem to indicate that DP is associated with a specific impairment in detecting facial happiness. Second, our DP cases may have adapted to the neutral face's expression in a neurotypical way (i.e., no adaptation), it is just that they only exhibit this PSE shift because their neural signal of happiness from the test faces is degraded due to abnormalities in their cortical face perception areas. The sadness signal from the amygdala, which is presumably intact in DP (Behrmann et al., 2007; Dinkelacker et al., 2010; Van den Stock et al., 2008), would thus have a stronger influence on our DP cases' judgments of emotion to the test faces. The resulting PSE shift could be explained due to this sadness signal not being counteracted by the perception of happiness from the cortical route in DP, rather than any differential effects of adaption to the neutral face *per se*. If this were the case, then it can explain why our DP cases were no different in their PSE values, consistency judgements and response times between the neutral and hybrid conditions: it is due to a common inability at being able to adapt to the LSF of the hybrid and neutral adaptors. While unpublished data by our lab indicates that no adaptation results in the same PSE and slope values as a neutral face adaptation condition in neurotypical individuals, it is as present unknown whether this holds true for DP cases. Future adaptation work should, therefore, take the cautionary measure of including a no adaptation baseline condition. This would give a pure PSE value from the test faces alone and allow researchers to confirm the suggestion that DP cases are adapting to the neutral face in a neurotypical way (i.e., no adaptation).

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

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

Conclusions

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

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6. Author Contributions

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

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