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Attentional modulation differentially affects ventral and dorsal face areas in both normal participants and developmental prosopagnosics

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ABSTRACT

Face-selective cortical areas that can be divided into a ventral stream and a dorsal stream. Previous findings indicate selective attention to particular aspects of faces have different effects on the two streams. To better understand the organization of the face network and whether deficits in attentional modulation contribute to developmental prosopagnosia (DP), we assessed the effect of selective attention to different face aspects across eight face-selective areas. Our results from normal participants found that ROIs in the ventral pathway (OFA, FFA) responded strongly when attention was directed to identity and expression, and ROIs in the dorsal pathway (pSTS-FA, IFG-FA) responded the most when attention was directed to facial expression. Response profiles generated by attention to different face aspects were comparable in DPs and normals. Our results demonstrate attentional modulation affects the ventral and dorsal steam face areas differently and indicate deficits in attentional modulation do not contribute to DP.

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Introduction

Faces contain a variety of information that is critical for effective social interaction. Expression, face viewpoint, and eye position change frequently over time, and these changeable aspects allow inferences about a person's current emotional state and the focus of their attention. In contrast, aspects such as identity and sex are constant over time, and they are often referred to as invariant aspects of faces (Haxby et al., 2000).

Our perception of these different aspects of faces depends on cortical areas that selectively respond to faces. Face-selective areas are found in the bilateral fusiform, the occipital lobe, along the superior temporal sulcus (STS), and in the frontal lobe (Duchaine & Yovel, 2015; Kanwisher et al., 1997). Haxby and colleagues (Haxby & Gobbini, 2011; Haxby et al., 2000) proposed an influential neurocognitive model that described the functions of areas in the face processing network, and Duchaine and Yovel (2015) suggested a revised model based on results from subsequent work. The revised model emphasized that face processing depends on two pathways. The ventral pathway, which includes the occipital face area (OFA), fusiform face area (FFA), and an area in anterior temporal lobe, preferentially processes form information, plays a primary role in representing invariant aspects of faces, and contributes to facial expression recognition (Dalrymple et al., 2011; Fox et al., 2009a; Ganel et al., 2005). The dorsal pathway consists of face-selective areas in posterior STS (pSTS-FA), anterior STS (aSTS-FA), and inferior frontal gyrus (IFG-FA), and these areas respond much more strongly to dynamic faces than to static faces (Fox et al., 2009b; Pitcher et al., 2011). The dorsal areas appear to play a key role in representing changeable aspects of facial features, though they may also contribute to perception of facial identity (Fox et al., 2011; Visconti di Oleggio Castello et al., 2017).

A key source of evidence indicating different face areas have distinct functions comes from investigations of the neural effects of modulations of face attention. In an early fMRI study, Hoffman and Haxby (2000) investigated the response of OFA, FFA and pSTS-FA in a task that required participants to selectively orient their attention to either facial identity (an invariant aspect) or eye gaze (a changeable aspect). They found bilateral OFA and bilateral FFA responded more strongly when participants attended to identity than eye gaze, whereas left pSTS-FA responded more

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strongly when gaze was attended than when identity was attended. These results provided support for the hypothesis that posterior ventral areas preferentially contribute to representation of invariant aspects whereas a posterior dorsal area is especially important for changeable aspects. In later studies, responses in pSTS-FA were again found to be stronger when participants attended to expression than to identity or sex (Dobs et al., 2018; Ganel et al., 2005; Narumoto et al., 2001), and responses of OFA and FFA were higher when attention was focused on sex than expression (Bernstein et al., 2018). In addition, a recent study reported that an anterior area in the dorsal pathway —IFG-FA—was strongly activated by attention to expression (Bernstein et al., 2018).

However, even though these studies relying face attention modulation have played an important role in theories about the division of labour in the face network, there are several issues that raise questions about their inferential value. First, face-selective areas in several papers were localized with nonstandard localizing contrasts rather than the more selective faces vs objects contrast (Fox et al., 2009b; Pitcher et al., 2011). For example, Hoffman and Haxby (2000) and Narumoto et al. (2001) used faces vs scrambled images while Dobs et al. (2018) used faces vs buildings, and these contrasts almost certainly generated ROIs that included a substantial proportion of voxels that would not be classified as face-selective in the more commonly used faces vs objects contrast. Second, most studies included fewer than 10 participants, and because many ROIs could not be identified in a substantial number of participants, findings for particular ROIs were often based on small samples (sometimes as small as five participants) (Bernstein et al., 2018; Hoffman & Haxby, 2000). Third, except for the most recent study (Bernstein et al., 2018), all previous studies only focused on the posterior face areas (OFA, FFA, pSTS-FA) and so included only one dorsal stream area. In our study below, we attempted to overcome these limitations to better investigate the functional roles of the ventral and dorsal face areas. Based on the models of face processing described above, we hypothesized that attention to different face aspects would differentially modulate responses in the two pathways.

In addition to investigating the effect of attention to different face aspects in neurotypical brains, we examined whether problems with attentional modulation play a role in developmental prosopagnosia (DP). DPs have great difficulty in recognizing face identity despite normal low-level vision and intellect and no history of brain damage (Behrmann et al., 2016; Susilo & Duchaine, 2013). A number of neural abnormalities have been identified in DP, including reduced responses to faces in face-selective areas (Furl et al., 2011; Jiahui et al., 2018), but no studies have investigated whether DPs have difficulties modulating their attention to faces and whether these deficits contribute to their impaired face recognition abilities. Face attention deficits could take many forms, and differences in face attentional deficits could contribute to the varied face processing profiles seen in DP (Biotti & Cook, 2016; Chatterjee & Nakayama, 2012; Marsh et al., 2019). For example, if an individual was impaired in attending to face identity but attended to other aspects of face information normally, this would lead to deficits with identity but typical processing of other face aspects. In contrast, another person might have deficits with identity and expression if they were unable to modulate their face network when required to process these aspects. Alternatively, face attention could fractionate along physical dimensions (e.g., left half vs right half; top half vs bottom half) in which case impairments to different aspects of face processing such as identity or expression would be dictated by the importance of the poorly attended face information for computations about that aspect. For example, deficits recognizing fearful facial expressions could result from poor attention to the upper half of the face (Schyns et al., 2002). Of course, it is possible we will find results that indicate DPs modulate their attention to faces normally, and this would suggest deficits in attentional modulation do not contribute to DP. To address whether DPs have face attentional modulation difficulties and whether these deficits contribute to their impaired face recognition abilities, we compared whether attentional modulation in face areas has similar effects in DPs and controls.

Materials and methods

Participants

Sixteen normal participants (Mean age = 42.0, 7 females) and 12 DPs (mean age = 44.8, 8 females)

were tested in this study (Figure S1, Table S1). DPs were recruited from www.faceblind.org All DPs reported problems with face recognition in daily life. DPs were assessed with the Cambridge Face Memory Test (CFMT) (Duchaine & Nakayama, 2006), a famous face test (Duchaine, Germine et al., 2007), and an old-new face discrimination test (Duchaine & Nakayama, 2005). All DPs except for one performed two or more standard deviations (S.D.) below the mean of published control results in at least two of the three diagnostic tests (Duchaine, Germine et al., 2007; Duchaine, Yovel, et al., 2007). The DP who did not reach −2 S.D. on two tests scored poorly on two of the three tasks (CFMT: $z = -1.9$; famous face: $z = -7.1$; old-new: $z = -0.5$), so we included her to increase the sample size. DPs were also accessed with Film Facial Expression Test (Banissy et al., 2011; Garrido et al., 2009; Lohse et al., 2016; Loth et al., 2018) to test their expression recognition ability. DPs' performance (mean = 0.86, S.D. = 0.06) was comparable to a group of 52 normal participants' (mean = 0.88, S.D. = 0.06) from Loth et. al., (2018). All participants had normal or corrected-to-normal vision and had no current psychiatric disorders. Participants provided written informed consent before doing the task, and all procedures were approved by Dartmouth's Committee for the Protection of Human Participants.

Stimuli and procedures

Participants did a one-back task during the attentional modulation experiment. The experiment included six runs in total. In each run, nine stimulus blocks that each lasted 18s each were interleaved with 18s fixation blocks. The experiment included three conditions (identity, expression, and view). Before each stimulus block began, a word that indicated the condition of the block was presented in the centre of the screen for three seconds. Participants pressed a button when the target aspect for a block (identity, expression, or view) was the same in two trials in a row (e.g., in expression blocks, participants needed to press the button when two smiling faces were shown back-to-back regardless of identity or face view). Each stimulus block included nine face images presented for 500 ms with a 1500 ms inter-stimulus interval (Figure 1A). Each image subtended approximately 7.2° × 9.5° of visual angle for width and height.

Before the attentional modulation experiment, each participant was scanned with a dynamic localizer containing five visual categories: faces, scenes, bodies, objects, and scrambled objects. Stimuli in the localizer were 1500 ms video clips. Faces and objects stimuli were drawn from stimuli used in Fox et al. (2009b), scene and body video clips were from Pitcher et al. (2011), and scrambled objects were created by scrambling the video clips of the objects spatially into 24 × 16 grids (Jiahui et al., 2018). Participants were scanned with five runs. In each 4.2-minute run, ten 12s stimuli blocks were interleaved by 12s fixation blocks. Each visual category was displayed twice in each scan in a quasi-random order across scans. In each category block, six video clips were presented interleaved by blank fixation screens presented for 500 ms. Stimuli were presented using Superlab 4.5.3 (www.superlab.com/) and displayed to the participant via a Panasonic DT- 4000UDLP projector (resolution: 1,024 × 768; refresh rate: 60 Hz) at the rear of the scanner.

MRI acquisition

Participants were scanned on a 3.0-T Phillips MR scanner (Philips Medical Systems, WA, USA) using a SENSE (SENSitivity Encoding) 32-channel head coil (see Jiahui et al., 2018 for more details). At the start of the scan, an anatomical volume was acquired using a high-resolution 3D magnetization-prepared rapid gradient-echo sequence (220 slices, field of view = 240 mm, acquisition matrix = 256 × 256, voxel size = 1 × 0.94 × 0.94 mm). Functional images were collected using echo-planar functional images (time to repeat = 2000ms, time echo = 35 ms, flip angle = 90°, voxel size = 3 × 3 × 3 mm). Each volume consisted of 36 interleaved 3-mm thick slices with 0-mm inter-slice gap. The slice volume was set to cover most of the brain including the entire temporal lobe. The location and extent of susceptibility effects are influenced by the slice orientation and phase-encoding direction (Ogawa et al., 1990; Ojemann et al., 1997). Here we used oblique slice orientation aligned with each participant's anterior commissure—posterior commissure (AC–PC) line, because it produces fewer susceptibility artifacts than the commonly used traverse orientation (Ojemann et al., 1997) and at the same time provides better coverage of the brain. The phase-encoding direction (anterior—

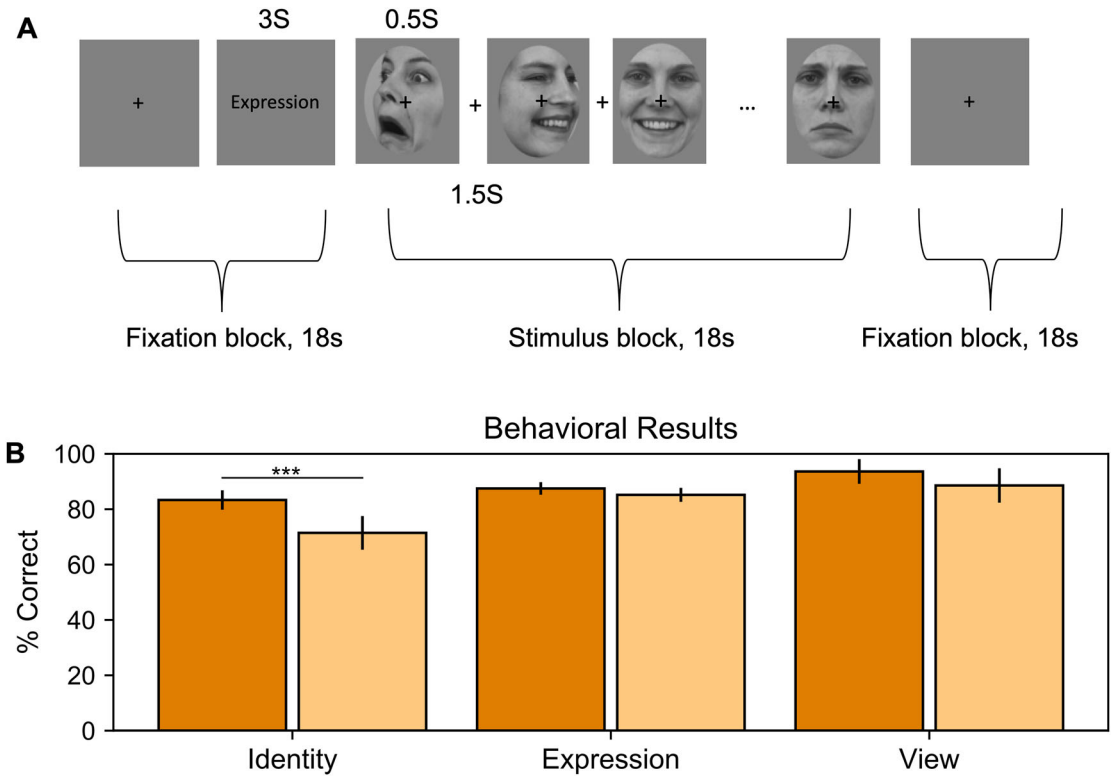

Figure 1. Experimental procedures and in-scanner behavioral results. (A) Example of the design of one scan. Each scan includes three conditions (identity, expression, or view) and the stimulus blocks (18s) were interleaved by the fixation blocks (18s). The word (identity, expression, or view) that was displayed for 3s before a block indicated the condition. Each image was presented for 0.5s, followed by a 1.5s inter-stimulus interval. (B) Participants did a one-back task in the scanner (identity, expression, or view). The in-scanner performance (Normals: identity (mean = 0.83, S.D. = 0.07), expression (mean = 0.88, S.D. = 0.05), view (mean = 0.94, S.D. = 0.09); DPs: identity (mean = 0.71, S.D. = 0.11), expression (mean = 0.85, S.D. = 0.04), view (mean = 0.89, S.D. = 0.11)) indicated both groups followed the experiment instructions. Error bars stand for 95% Confidence Intervals (CI) for each group in each condition. *** $p < 0.001$.

posterior) was chosen to reduce the signal loss in the more anterior part of the brain.

Data preprocessing

Data preprocessing was done using Freesurfer (https://surfer.nmr.mgh.harvard.edu/). Functional volumes were motion corrected and aligned to the anatomical volume for each participant. The aligned volume of each participant was resampled to the high-density surface mesh provided by Freesurfer, and then aligned to the standardized mesh of the template MNI305 FsAverage brain. The aligned functional volume was smoothed with a 4 mm FWHM (full width at half maximum) Gaussian kernel before analysis. Each voxel was fit with a general linear model (GLM) with one regressor per stimulus condition and the regressors for each stimuli condition were computed by modelling the hemodynamic response function (HRF). Following standard denoising procedures (Kay et al., 2013; Norman-Haignere et al., 2016), a linear-trend regressor and the first ten principal components from voxel responses in white matter were included to regress out signal drift and sources of noise with high variance across voxels as nuisance regressors in the model.

Data analysis

To avoid both the subjectivity of manually setting thresholds and the problem of how to deal with data from participants who have responses below typically used thresholds, we used the variable-window method to localize face-selective ROIs (Jiahui et al., 2018; Norman-Haignere et al., 2013, 2016; Saygin et al., 2016). We first made surface masks at the expected location for each face-selective ROI we planned to analyze. The mask was manually prepared by referring to the face-selective voxels of both groups at a liberal threshold ($P < 0.05$), in order

to include all voxels that could be considered part of a particular face-selective area. We then identified each participant's ROI by selecting the most selective voxels in the mask. To determine whether our results are consistent across different ROI sizes, we repeated our analysis at varied ROI sizes, ranging from 5 to 35% in 5% steps. Because this method does not use selectivity thresholds that an ROI must reach to be included in the analysis, it permits analysis of each ROI in each participant.

Bilateral OFA, FFA, pSTS-FA, and IFG-FA were localized with dynamic localizer runs. Responses to the three conditions (identity, expression, view) in the attentional modulation experiment runs were extracted from each ROI based on the top 10% most face-selective voxels in the dynamic localizer scans. Though we focus on the 10% most face-selective voxels, similar results were found when other percentages (from 5% to 35%) were systematically probed (Figure S2). To more thoroughly study of the ventral and dorsal face-selective areas, we attempted to include another two anterior ROIs (ATL-FA and aSTS) into analysis. However, we were unable to measure reliable attentional modulation responses in these two areas, presumably due to the susceptibility artifact caused by ear canal and due to the weak responses evoked by the design of attentional modulation task, and thus they were excluded from further analysis.

Results

Behavioral results

For most conditions (identity, expression, view), normal participants' and DPs' behavioral accuracy was between 83% and 94% for the in-scanner one-back task which indicated they attended to the target aspects (Figure 1B; Normals: identity (mean = 0.83, S.D. = 0.07), expression (mean = 0.88, S.D. = 0.05), view (mean = 0.94, S.D. = 0.09); DP: identity (mean = 0.71, S.D. = 0.11), expression (mean = 0.85, S.D. = 0.04), view (mean = 0.89, S.D. = 0.11)). Post-hoc analysis showed that normal participants' and DPs' accuracies were comparable for the expression and view conditions (Tukey Test; Expression: $z = 1.33$, $p = 0.19$; View: $z = 1.33$, $p = 0.19$), but not surprisingly, DPs performed significantly worse than normal participants in the identity condition (Tukey Test; $z = 3.50$, $p < 0.001$).

fMRI results

Differential attentional modulation in dorsal and ventral face areas in normal participants

To determine whether face areas in normal participants were modulated by attention to different aspects of faces, responses to each condition were extracted and statistically compared. For OFA, attentional modulation was found to be marginally significant between the three conditions in right OFA ($F(2,30) = 3.25$, $p = 0.05$). This effect resulted from a weaker response to view than identity or expression (see Table 1 for detailed Tukey Test stats). Attentional modulation was not significant in left OFA ($F(2,30) = 1.31$, $p = 0.28$). The attention modulation effect was significant in bilateral FFA (right FFA: $F(2,30) = 13.00$, $p < 0.001$; left FFA: $F(2,30) = 12.32$, $p < 0.001$). Responses during identity and expression blocks were comparable and were significantly stronger than the responses during view blocks (Table 1). We found significant attention modulation in all four bilateral dorsal face areas (right pSTS-FA: $F(2,30) = 16.15$, $p < 0.001$; left pSTS-FA: $F(2,30) = 18.41$, $p < 0.001$; right IFG-FA: $F(2,30) = 31.24$, $p < 0.001$; left IFG-FA: $F(2,30) = 21.59$, $p < 0.001$). The responses during expression blocks were significantly stronger

Table 1. Attentional modulation ANOVA stats in normal participants for each ROI.

	Normal Participants							
	One-way ANOVA		Identity-expression		Identity-view		Expression-view	
ROI	F(2,30)	*p*	*z*	*p*	*z*	*p*	*z*	*p*
rOFA	3.25	0.05	0.74	0.74	2.56	**0.03**	1.82	0.16
lOFA	1.31	0.28	0.91	0.63	1.67	0.22	0.76	0.73
rFFA	13.00	**<0.001**	−0.23	0.97	4.45	**<0.001**	4.67	**<0.001**
lFFA	12.32	**<0.001**	−0.14	0.99	4.37	**<0.001**	4.51	**<0.001**
rpSTS-FA	16.15	**<0.001**	−4.18	**<0.001**	1.48	0.30	5.66	**<0.001**
lpSTS-FA	18.41	**<0.001**	−6.26	**<0.001**	−3.4	**0.002**	2.84	**0.01**
rIFG-FA	31.24	**<0.001**	−1.40	0.34	6.26	**<0.001**	7.67	**<0.001**
lIFG-FA	21.59	**<0.001**	−4.59	**<0.001**	2.04	0.10	6.63	**<0.001**

than both identity and view in bilateral pSTS-FA and left IFG-FA (Table 1 and Figure 2A).

The individual ROI results indicate the dorsal and ventral face areas responded differently in the attentional modulation task. To quantitatively examine whether a division of labour between the ventral and the dorsal face pathways exists, responses from bilateral OFA and FFA were averaged to measure the ventral responses and responses from bilateral pSTS-FA and IFG-FA were combined to assess the dorsal responses. In ventral areas, responses to identity and expression were comparable (Tukey Test, z(identity—expression) = 0.44, $p = 0.90$, z(identity—view) = 3.76, $p < 0.001$, z(expression-view) = 3.32, $p = 0.003$). In contrast, responses to expression were the strongest among the three conditions in the dorsal pathway (Figure 3; Tukey Test, z(identity—expression) = −4.96, $p < 0.001$, z(identity—view) = 2.46, $p = 0.04$, z(expression-view) = 7.42, $p < 0.001$). A 2 (pathways) × 3 (conditions) ANOVA confirmed that these differences in the two pathways resulted in a significant interaction ($F(2,30) = 11.76$, $p < 0.001$). Results were

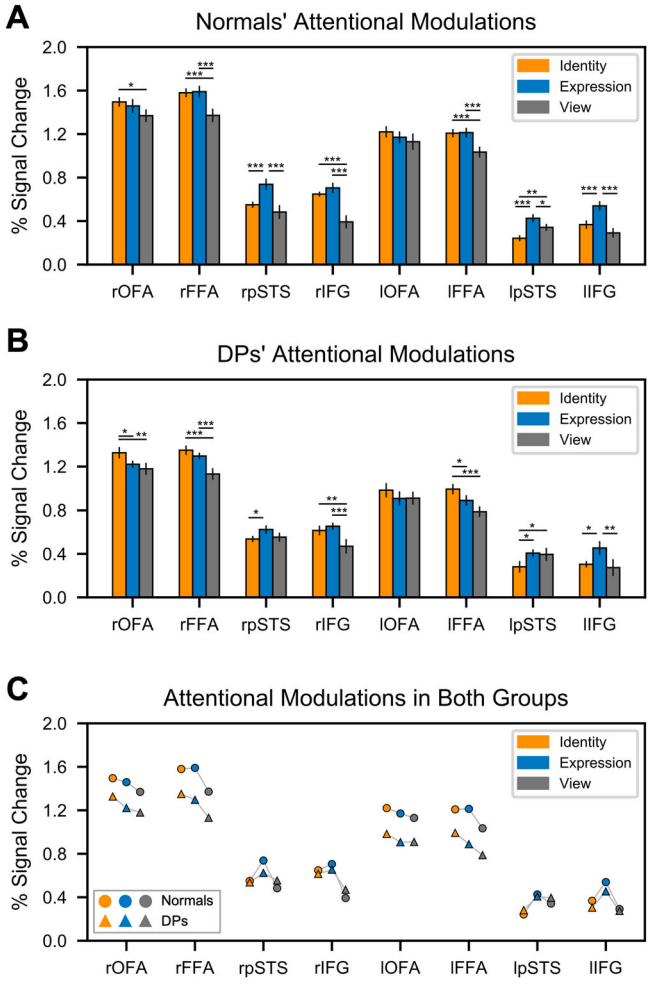

Figure 2. Attentional modulations for normal participants and DPs in each ROI. (A) Responses to the three conditions (identity, expression, or view) in bilateral face-selective ROIs in normal participants. (B) Responses to the three conditions (identity, expression, or view) in bilateral face-selective ROIs in DPs. Since absolute fMRI response magnitudes can vary substantially across subjects due to factors unrelated to the neural response to a stimulus category (e.g., vascularization), the error bars were calculated to display the variance of the three conditions (95% CI of each condition in each ROI; "within-subject" SEs, (Loftus & Masson, 1994)). Thus, the two groups were plotted on different axes, and the error bars should not be used to compare the absolute response magnitudes between normals and DPs. (C) To directly compare the response profiles between the two groups in each ROI, the responses for the two groups were plotted together. Because the within-subject SEs were not suitable to compare the two groups, error bars were omitted in this panel. The detailed ROI-by-ROI comparison of response profiles between the normal participants and DPs found a significant difference in response profiles only in right pSTS-FA ($F(2,22) = 3.76$, $p = 0.04$) due to a weaker response to expression in DPs. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$.

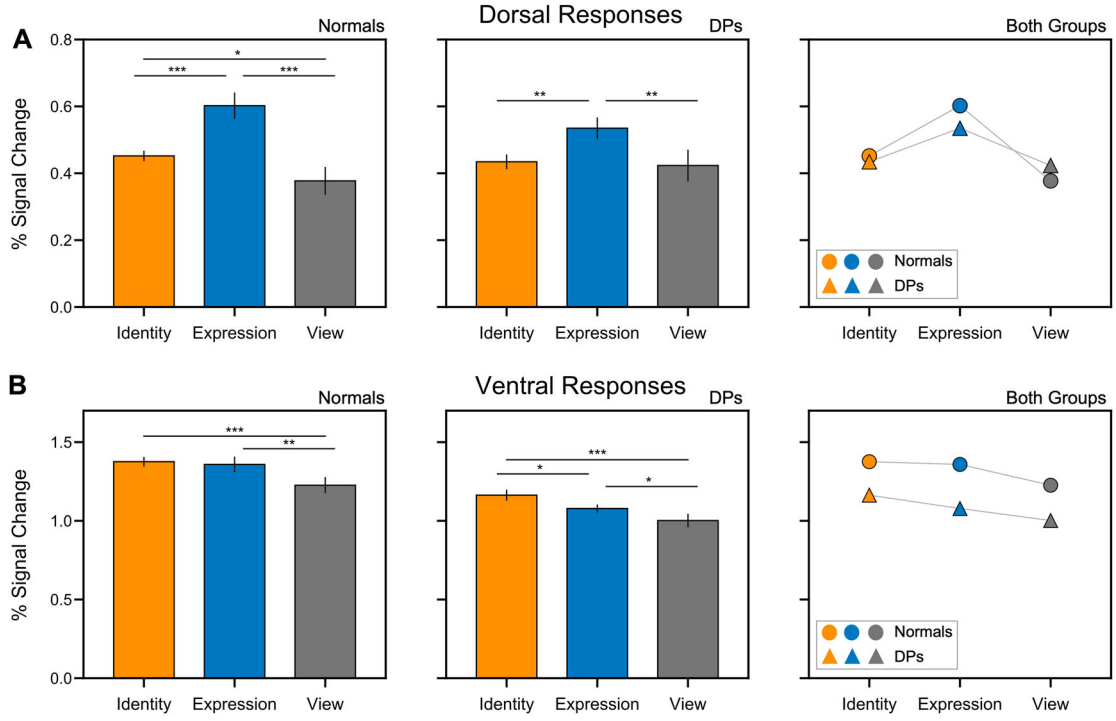

Figure 3. Responses to identity, expression, and view conditions in the dorsal and ventral face-selective ROIs. (A) Responses in the dorsal ROIs (bilateral pSTS-FA and IFG-FA). (B) Responses in the ventral ROIs (bilateral OFA and FFA). The left panels display results for normal participants, the middle panels show results for DPs, and the responses of the groups are plotted together in the right panels. The response profiles in both groups were very similar. Because absolute fMRI response magnitudes vary across subjects due to factors unrelated to the neural response to a stimulus category, the error bars were calculated to display the variance of the three conditions (95% CI of each condition in each ROI; "within-subject" SEs, (Loftus & Masson, 1994)) and so error bars in the column graphs are within-subject SEs (95% CI of each condition). Figures for each group were plotted in separate plots, and the error bars should not be used to compare the absolute response magnitudes between normals and DPs. In the figures on the right, the two groups are displayed together to allow direct comparison between the response profiles for each group. Error bars were again omitted. Comparisons of response profiles between the two groups found marginal significance in the dorsal pathway ($F(2,52) = 3.06$, $p = 0.08$) that was mainly due to a weaker response to expression in DPs. ***$p < 0.001$, **$p < 0.01$, *$p < 0.05$.

similar if we split the two pathways to only include left or right hemisphere ROIs.

DPs participants have a similar division of labour between the dorsal and ventral stream face areas as normal participants

Next, we tested whether face areas in DP participants are modulated by task and whether those modulations are comparable to those found in normal participants.

Like normal participants, bilateral OFA was subtly modulated by attention to different aspects of faces (right OFA: $F(2,22) = 5.80$, $p = 0.01$; left OFA: $F(2,22) = 1.06$, $p = 0.36$). Attention modulation was significant in all other ventral and dorsal ROIs (right FFA: $F(2,22) = 16.18$, $p < 0.001$; left FFA: $F(2,22) = 10.60$, $p < 0.001$; right pSTS-FA: $F(2,22) = 3.76$, $p = 0.04$; left pSTS-FA: $F(2,22) = 4.34$, $p = 0.03$; right IFG-FA: $F(2,22) = 8.82$, $p = 0.007$; left IFG-FA: $F(2,22) = 6.01$, $p = 0.02$). In bilateral FFA, responses to identity and expression were significantly stronger than the responses to view (Table 2). In bilateral pSTS-FA and IFG-FA, responses to expression blocks were the strongest, similar to what was found in the normal participants (Table 2 and Figure 2B).

To determine whether normal and DP participants showed different patterns of modulation, a 3 (condition) × 2 (group) ANOVA was performed for each ROI. This analysis found that the interaction was not significant in seven of the eight ROIs. The one exception was right pSTS-FA ($F(2,52) = 4.57$, $p = 0.03$). This significant difference was driven primarily by a weaker response to expression in DPs than controls. However, the pattern in right pSTS-FA for the two groups was similar, with both groups

Table 2. Attentional modulation ANOVA stats in DP participants for each ROI.

	DP Participants							
	One-way ANOVA		Identity-expression		Identity-view		Expression-view	
ROI	F(2,22)	*p*	*z*	*p*	*z*	*p*	*z*	*p*
rOFA	5.80	**0.01**	2.47	**0.04**	3.45	**0.002**	0.98	0.59
lOFA	1.06	0.36	1.34	0.37	1.30	0.40	−0.05	1.00
rFFA	16.18	**<0.001**	1.40	0.34	5.70	**<0.001**	4.30	**<0.001**
lFFA	10.60	**<0.001**	2.44	**0.04**	4.81	**<0.001**	2.37	0.05
rpSTS-FA	3.76	**0.04**	−2.71	**0.02**	−0.54	0.85	2.17	0.08
lpSTS-FA	4.34	**0.03**	−2.79	**0.01**	−2.52	**0.03**	0.26	0.96
rIFG-FA	8.82	**0.007**	−0.88	0.65	3.28	**0.003**	4.16	**<0.001**
lIFG-FA	6.01	**0.02**	−2.81	**0.01**	0.57	0.83	3.38	**0.002**

showing the strongest response in the expression condition (Figure 2). These results across the ROIs demonstrate that face areas in DPs are modulated by task, and the similar response profiles in DPs and normal participants suggest DPs' deficits with faces do not result from deficits with face attentional modulation.

As we did for normal participants, we combined the bilateral OFA and FFA as ventral stream areas, and bilateral pSTS-FA and IFG-FA as dorsal stream areas. Like normal participants, response profiles of the ventral stream and dorsal stream areas were significantly different ($F(2,22) = 33.60$, $p < 0.001$). In the ventral stream areas, responses to identity were the strongest, followed by responses to expression and then to view (Figure 3; Tukey Test, z(identity—expression) = 2.73, $p = 0.02$, z(identity—view) = 5.19, $p < 0.001$, z(expression-view) = 2.46, $p = 0.04$). In the dorsal steam areas, responses to expression was the strongest (Tukey Test, z(identity—expression) = −3.21, $p = 0.004$, z(identity—view) = 0.35, $p = 0.93$, z(expression-view) = 3.56, $p = 0.001$).

Next, we carried out a 3 (condition) × 2 (group) ANOVA for each pathway to compare whether the response profiles were different between DPs and normal participants. Non-significant interactions of conditions and groups showed that DPs had similar response profiles as normal participants in both ventral ($F(2,52) = 0.85$, $p = 0.43$) and dorsal ($F(2,52) = 3.06$, $p = 0.08$) areas. Analysis of ventral or dorsal areas in only the left hemisphere or only the right hemisphere showed similar results.

The analyses above were concerned with attentional modulation, we then tested whether controls and DPs differed in the overall strength of their activations in the ROIs analyzed. No group differences between the response magnitude for normal participants and DPs was found in any of the ROIs or in any pathways.

Discussion

Attentional modulation in normal participants

We hypothesized that attention to different face aspects would modulate responses in the ventral and dorsal pathways in different ways. In our results, OFA and FFA responded strongly when attention was directed to face identity and expression, whereas pSTS-FA and IFG-FA responded most strongly when attention was focused on facial expression. In addition to analyzing individual ROIs, we combined the results from the four ROIs in each pathway to calculate a single measure of the profile for each pathway. Unlike previous studies that assessed the dorsal stream using only results from pSTS-FA (Bernstein et al., 2018; Dobs et al., 2018; Ganel et al., 2005; Narumoto et al., 2001), the results of this combined analysis better demonstrates the division of labour between the two pathways.

We found responses to identity blocks and expression blocks were comparable in the ventral face ROIs. This finding fits with the predictions of the Haxby et al. (2000) model which proposes OFA serves as a gateway for both the ventral and dorsal streams and thus contributes to the representation of both changeable and static aspects of faces (See also Pitcher et al., 2008; Rossion et al., 2003). However, the Haxby model also proposes that FFA processes the static aspects of faces (e.g., identity) but not changeable aspects, so it suggests FFA should show a stronger response during identity blocks than expression blocks. In contrast, FFA's comparable response to identity and expression blocks is

consistent with the revised model of face processing mentioned earlier (Duchaine & Yovel, 2015). The revised model's characterization of FFA was motivated by evidence indicating FFA also plays a role in the processing of facial expression. For example, a patient with a right FFA lesion but spared right OFA and right pSTS-FA performed poorly on tests of facial expression recognition (Dalrymple et al., 2011). In addition, an earlier attention modulation study found stronger responses in FFA when expression was attended than when identity was attended (Ganel et al., 2005), and FFA was sensitive to differences in facial expression in an fMRI-adaptation task (Fox et al., 2009a; Xu & Biederman, 2010). Taken together, it appears that OFA and FFA both contribute to expression processing.

Face viewpoint was the other dynamic face aspect we investigated. Response during viewpoint blocks tended to be weak in the dorsal areas, and though the responses in our participants during the face-view blocks was not always significantly lower than the responses to the other two conditions, the responses were never the highest in any of the ROIs. Although we cannot be certain, differential task difficulty may have contributed to the weaker response in the face-view task, because behavioral accuracy during viewpoint blocks was the highest among the three conditions in both normal participants and DPs (see Figure 1; Tukey Test, normals: z(identity—expression) = −1.70, $p = 0.20$, z(identity—view) = −4.21, $p < 0.001$, z(expression-view) = −2.51, $p = 0.03$; DPs: z(identity—expression) = −4.23, $p < 0.001$, z(identity—view) = −5.28, $p < 0.001$, z(expression-view) = −1.05, $p = 0.55$).

Attentional modulation in DP participants

The DP participants had similar response profiles as normal participants in all eight face-selective ROIs. This similarity indicates that the organization of the face processing network in DPs and normal participants is comparable. DPs, like controls, appear to rely on ventral areas for identity and expression processing and on dorsal areas for expression perception. Their normal attentional modulations suggest that DPs' deficits with faces do not result from problems in selectively attending to task-relevant aspects of faces. These results are consistent with several other studies showing that DPs and normal participants have similar functional architectures for face recognition. For example, when famous faces were successfully recognized, DPs and controls produced the same series of event-related potential components (Eimer et al., 2012), and a previous fMRI study found that the locations of peak activation in 12 face-selective areas in DPs and controls were nearly identical (Jiahui et al., 2018). While there may be a small proportion of DPs who have qualitatively different face architectures, most DPs seem to rely on the same set of mechanisms to process faces as normal participants. However, the numerous studies reporting abnormal functional responses in DPs including decreased face selectivity (Furl et al., 2011; Jiahui et al., 2018), functional connectivity (Lohse et al., 2016; Song et al., 2015; Zhao et al., 2016), and atypical event-related potentials (Fisher et al., 2016; Towler & Eimer, 2012; Towler et al., 2016) indicates that the face network, while intact, does not operate effectively in DPs.

In addition to comparing the modulations between DPs and the normal participants, we were interested to see whether the two groups differ in the strength of their responses to faces in the face ROIs as found in previous studies (Furl et al., 2011; Jiahui et al., 2018). Though the response amplitudes of the ventral regions are lower in DPs than in normal participants, statistical comparison of the response magnitude between the two groups did not show significant group differences in any of the ROIs or either pathway (Figures 2 and 3). These results differ from the recent study from our group mentioned earlier in which we found that a group of 22 DPs, 12 of whom participated in the current study, had decreased face selectivity in a number of ventral and dorsal face areas that were driven by weaker responses to faces rather than stronger responses to objects. The attentional modulation task requires participants to allocate their attention to a certain aspect of the face, rather than allowing them to freely search the face in a natural way as what they usually do in a dynamic localizer task. Because the response to faces in all the ventral areas was weaker in the DPs than the controls in the current study, we suspect that the absence of a group difference in the response to the faces in the attentional study resulted from either the smaller sample size, the task, the use of static faces, or some combination of these factors. However, the

comparable response to faces in DPs and controls in the dorsal areas is surprising, because in our previous study (Jiahui et al., 2018), DPs showed reduced responses to faces in both right pSTS-FA and right IFG-FA relative to controls. Given that responses in dorsal face areas are greatly enhanced by dynamic stimuli (Fox et al., 2009b; Pitcher et al., 2011), it is plausible that differences in the tasks, the presence or absence of face movement, or their combination may account for the inconsistent findings, but definitely answering this question will require further studies.

Summary

With broader coverage of ventral and dorsal face areas and a larger sample size than previous studies, we found selective attention to particular aspects of faces differentially modulated the ventral and dorsal face areas in a manner consistent with a revised model of face processing that proposes that ventral areas contribute to both identity and expression processing whereas dorsal areas are especially important for expression processing (Duchaine & Yovel, 2015). The similarity of the modulation profiles in both pathways for normal participants and DPs indicates that DPs' behavioral deficits are not due to problems with attentional modulation.

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