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Normal perception of Mooney faces in developmental prosopagnosia: Evidence from the N170 component and rapid neural adaptation

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Abstract

Individuals with developmental prosopagnosia (DP) have a severe difficulty recognising the faces of known individuals in the absence of any history of neurological damage. These recognition problems may be linked to selective deficits in the holistic/configural processing of faces. We used two-tone Mooney images to study the processing of faces versus non-face objects in DP when it is based on holistic information (or the facial gestalt) in the absence of obvious local cues about facial features. A rapid adaptation procedure was employed for a group of 16 DPs. Naturalistic photographs of upright faces were preceded by upright or inverted Mooney faces or by Mooney houses. DPs showed face-sensitive N170 components in response to Mooney faces versus houses, and N170 amplitude reductions for inverted as compared to upright Mooney faces. They also showed the typical pattern of N170 adaptation effects, with reduced N170 components when upright naturalistic test faces were preceded by upright Mooney faces, demonstrating that the perception of Mooney and naturalistic faces recruit shared neural populations. Our findings demonstrate that individuals with DPs can utilize global information about face configurations for categorical discriminations between faces and non-face objects, and suggest that face processing deficits emerge primarily at more fine-grained higher-level stages of face perception.

Developmental prosopagnosia (DP) is a selective impairment in face recognition which occurs in the context of normal low-level vision and intellectual ability and in the absence of obvious neurological damage (see Towler & Eimer, 2012; Susilo & Duchaine, 2013; for recent reviews). Alongside their core deficit in recognising familiar individuals, individuals with DP may or may not show impairments in other aspects of face processing. Some DPs perform poorly on face matching tasks with little or no memory load, indicative of deficits in on-line face perception, while others perform within the normal range on face perception tasks (Duchaine et al., 2007; Duchaine, 2011). Individual DPs have also been documented to have difficulties with recognising expressions of emotion (Duchaine et al., 2003; 2006) or detecting the presence of a face, while other DPs appear normal at these tasks (Le Grand et al., 2006; Garrido et al., 2008). Such selective impairments in specific aspects of face processing support cognitive and neural models which postulate some division of labour among the brain systems that encode different aspects of faces (Bruce and Young, 1986; Haxby et al., 2000), and the study of developmental prosopagnosia can be a powerful tool for demonstrating dissociations between different aspects of face perception and recognition (Duchaine & Nakayama, 2006; Duchaine, 2011).

The heterogeneous pattern of face processing problems in DP suggests their core impairment in familiar face recognition may not be tied to a single underlying deficit. One suggestion that has recently received considerable attention is that many cases of developmental prosopagnosia are due to specific impairments in configural or holistic aspects of face processing. While early stages of local feature-based face perception (processing of contours, shapes, and individual facial features) are intact, subsequent higher level processing stages which integrate information from visual features over larger regions of the visual field (e.g. Maurer et al., 2002; Rossion, 2009) may operate differently in DPs (e.g. Avidan et al., 2011; Palermo et al., 2011). Support for this hypothesis comes from a number of studies which have investigated the configural processing of faces, and found differences between individuals with and without DP. The fact that stimulus inversion strongly impairs face recognition (e.g., Yin, 1969) is often interpreted as evidence for configural face

processing. Inversion preserves the physical information contained within an image, but disrupts the prototypical first-order configuration of faces (e.g., eyes above nose, nose above mouth; Maurer et al., 2002). Relative to participants with unimpaired face recognition, individuals with DP tend to have smaller face inversion effects in tasks involving identity perception (Duchaine et al., 2007; 2011), and this has been attributed to an impairment in the mechanisms which are specifically tuned to analyse upright faces. Similar differences between DPs and controls have been found in studies that were specifically designed to investigate markers of holistic face processing. When asked to match the identity of the top half of face pairs and ignore their bottom halves, control participants display interference from the task-irrelevant bottom half when the two halves are spatially aligned relative to trials where they are misaligned, suggesting that aligned face halves are integrated into a coherent new holistic face representation (Young et al., 1987; Hole et al., 1994). By comparison, this composite face effect tends to be reduced in individuals with DP (Palermo et al., 2011; Avidan et al., 2011). Another demonstration of the effects of holistic face processing comes from the part-whole task (Tanaka et al., 1993). For neurotypical individuals, performance in sequentially matching face parts is better when these are presented in the context of an upright face than when they are shown in isolation or when the configuration of the facial features is scrambled (Tanaka et al., 1993). Like control participants, DPs also match mouths better when they are presented in a face, but interestingly they show no benefit of face context when matching the eye region (DeGutis et al., 2012). This lack of recognition benefit for viewing the eyes in the context of a whole face is reminiscent of children with autistic spectrum disorder (ASD; Joseph & Tanaka, 2003). However, DP and ASD have also been shown to be separate and distinct disorders (Duchaine et al., 2008).

Mooney faces (Mooney, 1957) provide a different way to investigate holistic aspects of face processing. These two-tone images can be readily perceived as faces, even though they do not include face parts that are recognizable in isolation (see Figure 1B). The perception of Mooney faces is assumed to be based on the integration of information across separate regions of the image, resulting in a holistic representation of the configuration of a face (Latinus and Taylor, 2005; 2006).

Accordingly, inverted Mooney faces are typically not recognized as faces or any other meaningful object. There is at least one documented case of an acquired agnosic patient with prosopagnosia who demonstrated severe difficulties in detecting Mooney faces (Steeves et al., 2006), indicating that holistic aspects of face perception that are required for the basic level categorisation of Mooney faces can be affected in some cases of prosopagnosia. If DP is linked to impaired holistic face processing, individuals with DP may also show difficulties in categorising Mooney faces as faces. However, one previous behavioural study found that the detection of Mooney faces appeared to be normal in a group of eight DPs (Le Grand et al., 2006). Given the heterogeneity of face processing deficits in DP, it is unclear whether the preserved ability to recognize Mooney faces is generally common in DP. It is also unclear whether the neural processes that underlie the perception of Mooney faces are the same in individuals with DP and in individuals with unimpaired face recognition abilities. The aim of the present study was to measure event-related brain potential (ERP) correlates of visual face processing in response to Mooney faces in a group of sixteen individuals with DP in order to test whether they are the same or different from the neural signatures of Money face processing in unimpaired individuals.

Evidence for configural or holistic face processing at early stages of visual analysis comes from ERP studies that measured the face-sensitive N170 component. The N170 is a visual evoked brain potential which is larger in amplitude to faces than non-face objects (e.g. Bentin et al., 1996). Source localisation studies (Bötzel, 1995; Rossion et al., 2003; Itier and Taylor, 2004; Watanabe et al. 2003) have suggested that the N170 component is generated in structures such as the middle fusiform gyrus, inferior occipital gyrus and the superior temporal sulcus, brain regions all known to be involved in face-selective processing from neuroimaging studies (e.g. Haxby et al., 2000). The N170 component occurs 140-200ms after stimulus onset and is thought to reflect early perceptual structural encoding stages that precede face recognition and identification (Eimer, 2000a). The N170 is not exclusively linked to one single specific aspect of visual face perception, but can reflect distinct but temporally overlapping stages of face processing. The fact that the N170 is triggered in response

to single features such as isolated eyes (e.g., Bentin et al., 1996) suggests that this component is linked to neural mechanisms involved in the detection of prominent facial features. However, other results demonstrate that the N170 is not exclusively associated with part-based face processing. The N170 component is highly sensitive to the orientation of faces, with larger amplitudes and longer latencies for inverted as compared to upright naturalistic faces (Rossion et al., 1999; Eimer, 2000), demonstrating links between the N170 and configural face processing. Evidence that the N170 component is also linked to holistic aspects of face perception comes from the observation that Mooney faces trigger larger N170 amplitudes than non-face Mooney objects (George et al., 2005; Eimer et al., 2011). The N170 is has also been found to be larger to upright as compared to inverted Mooney faces (Latinus & Taylor, 2005), even though these images are almost identical in terms of their low-level properties. These observations suggest that face-selective neuronal populations respond preferentially to the holistic percept of Mooney faces in a canonical orientation, and that these responses are disrupted when Mooney faces are inverted.

Given these well-documented links between the N170 component and face-sensitive stages of visual processing, the question whether this component is intact or atypical in individuals with DP is clearly important. Demonstrating that the N170 shows an unusual pattern in response to different manipulations of visual face processing in individuals with DP would strongly suggest that at least some of the face recognition impairments in DP are due to deficits in early perceptual stages of face processing. Reduced or absent face-sensitivity of the N170 component has been found in some individuals with DP (e.g. Bentin et al., 1999; Németh et al, 2014), and additionally in individuals who were deprived of patterned visual input for the first few months of life due to congenital cataracts (Röder et al., 2013). However, a previous study from our lab showed that DPs generally have normal face-sensitive N170 components in response to naturalistic photographs of faces versus non-face objects (Towler et al., 2012). But this does not necessarily imply that the processing of first-order configural information about a face is intact in DP, as N170 amplitude enhancements to faces versus non-face objects may exclusively reflect the part-based processing of prominent facial features such

as the eyes (e.g., Bentin et al., 1996). In fact, the DPs tested in our study (Towler et al., 2012) failed to show the normal effect of face inversion on N170 amplitudes with naturalistic faces. While N170 components are typically enhanced for inverted faces, there were no N170 amplitude differences between upright and inverted faces in the DP group. This observation suggests that at least some aspects of configural face processing do not operate in the typical fashion in individuals with DP, although this study cannot rule out the additional contribution of facial feature inversion.

The goal of the present study was to obtain further insights into possible perceptual face processing deficits in DP by measuring N170 components to upright Mooney faces, inverted Mooney faces, and Mooney houses in the same group of sixteen individuals with DP that took part in our previous experiment with naturalistic face images (Towler et al., 2012). As the perception of Mooney stimuli as faces is assumed to reflect holistic face processing, an atypical pattern of N170 responses to Mooney faces would suggest that this aspect of face perception is impaired in DP. To study the response profile of the N170 component in response to Mooney faces in DP, we used a rapid neural adaptation procedure that was identical to the procedure used in an earlier experiment with participants without face recognition impairments (Eimer et al., 2011). Adaptor stimuli (S1) and test stimuli (S2) were presented successively for 200 ms each, and were separated by a 200 ms inter-stimulus interval (Figure 1A). Upright Mooney faces, inverted Mooney faces, or upright Mooney houses were used as adaptor stimuli, and upright naturalistic face photographs served as test stimuli (Figure 1C). N170 components were measured independently for the three types of adaptors, and for the naturalistic face test stimuli. To keep participants' attention focused on all stimuli, they were instructed to monitor the display for infrequent target stimuli that contained a red border around the image.

The logic of the procedure was that if Mooney face adaptors and naturalistic face test stimuli trigger overlapping neural populations, N170 adaptation (i.e., reduced N170 amplitudes) will be observed in response to the test stimuli. If they do not activate shared neural populations, no such adaptation

effect will be observed (e.g. Grill-Spector et al., 2006, for applying the same logic to fMRI adaptation; and Eimer, Kiss, & Nicholas, 2010, for rapid adaptation effects on the N170 component). The extent to which representations of Mooney and naturalistic faces share overlapping neural populations will be reflected by the extent of N170 adaptation for naturalistic face test stimuli. Figure 1C shows the results from our previous study (Eimer et al., 2011). We found that N170 amplitudes to naturalistic face test stimuli were reduced when they were preceded by upright Mooney faces as compared to Mooney houses, indicating that the face-selective neurons which encode upright Mooney faces at sensory-perceptual stages are also recruited during normal face perception. There was also some N170 adaptation when naturalistic faces were preceded by inverted Mooney face adaptors, but this effect was smaller than the effect observed with upright Mooney faces. Furthermore, and in line with previous findings (George et al., 2005) the N170 to upright Mooney face adaptors was larger than the N170 to Mooney houses. N170 amplitudes did not differ in amplitude from the N170 to inverted Mooney faces (see also Latinus & Taylor, 2006). These results show that in participants with unimpaired face recognition, upright Mooney faces and naturalistic faces activate shared face-sensitive neural populations.

If individuals with DP were unable to process holistic information about the presence of a face in the absence of independently recognizable facial features, a different pattern of results should be observed in this study. The absence of N170 amplitude differences between upright or inverted Mooney faces and Mooney houses would suggest that face-specific neural populations are not selectively activated by Mooney faces in DPs. This would be further confirmed by the absence of N170 adaptation effects in response to naturalistic face test stimuli (i.e., no N170 amplitude differences for upright faces preceded by upright Mooney faces, inverted Mooney faces, or Mooney houses, respectively). Alternatively, it is possible that DPs show normal face-sensitive N170 components in response to Mooney faces, and N170 adaptation effects that are similar to those observed in our previous study for participants without face recognition impairments (Eimer et al., 2011; see Figure 1C). This would suggest that face-selective perceptual processing mechanisms

operate normally in DP even for Mooney faces versus non-faces, when these mechanisms cannot be based on the detection of specific facial features, but have to rely solely on holistic information about the presence of face-like configurations in two-tone images.

Method

Participants

Sixteen participants with DP (12 female) were tested. Their age ranged between 22 and 67 years (mean age: 40 years). All reported severe difficulties with face recognition since childhood. They were recruited after contacting our research website (http://www.faceblind.org). To assess and verify their reported face recognition problems, behavioural tests were conducted in two sessions on separate days, prior to the EEG recording session. To rule out deficits in basic visual functioning as cause of their face recognition deficits, the DPs completed the low-level visual-perceptual tests of the Birmingham Object Recognition Battery (Riddoch & Humphreys, 1993). Test performance was within the normal range for all DPs tested.

Recognition of famous faces were measured with the Famous Face Test (FFT; Duchaine & Nakayama, 2005): DPs were shown images of 60 celebrities from entertainment, politics, or sports, which were cropped so that little hair or clothing was visible. At the end of the test, DPs were read the names of those individuals that they failed to recognize, and asked whether they had seen their face repeatedly in everyday life. Only previously seen famous faces were used to calculate recognition performance. Table 1 shows recognition percentage for famous faces in the FFT, separately for each of the sixteen DPs tested. As expected, DPs generally performed poorly in this test, with an average face recognition rate of 33.5% (ranging between 13.3% and 60% for individual

DPs). For participants with unimpaired face recognition abilities, the average recognition rate is above 90% for the same set of famous faces (Garrido et al., 2008).

Table 1 also shows z-scores of the performance of all 16 DPs in other behavioural face processing tests. In the Cambridge Face Memory Test (CFMT), faces of six target individuals shown in different views are memorized, and then have to be distinguished from two simultaneously presented distractor faces (see Duchaine & Nakayama, 2006a, for a full description). In the Old-New Face Recognition test (ONT; Duchaine & Nakayama, 2005), ten target faces (young women photographed under similar conditions and from the same angle) are memorized. In the test phase, target faces and 30 new faces are presented in random order, and an old/new discrimination is required for each face. In the Cambridge Face Perception Test (CFPT; Duchaine, Yovel, & Nakayama, 2007), one target face in three-quarter view is shown above six frontal-view morphed test faces that contain a different proportion of the target face and have to be sorted according to their similarity to the target face. Faces are presented either upright or inverted (shown separately in Table 1). As can be seen from the z-scores in Table 1, all DPs were impaired in the CFMT, and all except one in the ONT. There was also some evidence for face perception deficits in the CFPT, and these appeared more pronounced for upright faces than for inverted faces.

Additionally, all DP participants performed an Old-New Recognition test for houses in order to ascertain the extent of their object recognition deficits. In the Old-New House Recognition test (Duchaine & Nakayama, 2005), ten target houses are memorized. In the test phase, target houses and 30 new houses are presented in random order, and an old/new discrimination is required for each house. Four out of the sixteen DP participants were significantly impaired in this task and were more than -2 z-scores below the mean (CM, AH, KS, & MZ). Three out of these four participants with object recognition deficits showed numerically greater impairments in the faces version of the ONT than in the houses version.

Stimuli and procedure

Two different sets of stimuli (adaptors and test stimuli) were employed. Adaptors were two-tone Mooney stimuli from different categories (upright faces, inverted faces, houses). Test stimuli were upright naturalistic faces. Each of these four stimulus categories included 12 individual images. Naturalistic faces were images of 12 different individuals (6 male, 6 female) with neutral expression from a standard set of faces (Ekman & Friesen, 1976). Upright and inverted Mooney faces were taken from the original Mooney face stimuli (Mooney, 1957). Mooney houses were created from naturalistic images of houses by using Adobe Photoshop CS3 to generate two-tone images that were equivalent in terms of low-level visual properties to the Mooney faces. Angular size was 2.68°× 4.75° for all Mooney stimuli and 2.68° × 4.57° for naturalistic faces. Average luminance was 68 cd/m^2 for Mooney stimuli and 21 cd/m^2 for naturalistic faces. On each trial, two images (S1: adaptor stimulus; S2: test stimulus) were presented successively for 200 ms each, separated by a 200 ms interstimulus interval (Figure 1A). Upright Mooney faces, inverted Mooney faces and houses were presented with equal probability as S1. Only naturalistic upright faces were presented as S2 (Figure 1B). The intertrial interval was 1500 ms. The experiment included four experimental blocks with 108 trials per block. Each block contained 36 trials for each of the three S1 categories, which were presented in random order. Response-relevant targets were defined by the additional presence of a red rectangular outline shape aligned with the outer contours of either an S1 or S2 stimulus. Participants were required to press button on a response pad when they detected a response-relevant target. All other trials required no behavioural response. Each block contained 12 targets (with four target trials for each of the three S1 categories), which were equally likely to be presented as S1 or S2.

EEG recording and data analysis

EEG was DC-recorded with a BrainAmps DC amplifier (upper cut-off frequency 40 Hz, 500 Hz sampling rate) and Ag-AgCl electrodes mounted on an elastic cap from 23 scalp sites (Fpz, F7, F3, Fz, F4, F8, FC5, FC6, T7, C3, Cz, C4, T8, CP5, CP6, P7, P3, Pz, P4, P8, PO7, PO8, and Oz, according to the extended international 10-20 system). Horizontal electrooculogram (HEOG) was recorded bipolarly from the outer canthi of both eyes. An electrode placed on the left earlobe served as reference for online recording, and EEG was re-referenced off-line to a common average reference. Electrode impedances were kept below 5 kΩ. EEG data were analysed for nontarget trials only, to avoid contamination with response-related brain activity. EEG was epoched offline from 100 ms before to 700 ms after S1 onset. Epochs with activity exceeding ±30 μV in the HEOG channel (reflecting horizontal eye movements) or ±60 μV at Fpz (indicating eye blinks or vertical eye movements) were excluded from analysis, as were epochs with voltages exceeding ±80 μV at any other electrode, and trials with manual responses. Following artefact rejection, EEG waveforms were averaged separately for S1 and S2 stimuli, separately for trials with upright Mooney face adaptors, inverted Mooney face adaptors, and Mooney house adaptors, resulting in six sets of averaged ERP waveforms. N170 components in response to S1 and S2 stimuli were measured at lateral posterior electrodes P7 and P8. For ERPs in response to S1, a 100 ms pre-stimulus baseline was used. For ERPs in response to S2, we employed a 100 ms baseline from 50 ms before to 50 ms after S2 onset. N170 mean amplitudes were quantified within a 150–190 ms time interval following S1 or S2 onset. Repeated-measures analyses of variance (ANOVAs) were performed on N170 mean amplitude measures.

Results

Behaviour

Developmental prosopagnosic participants detected 96% of all target trails which contained an additional red rectangle around either the S1 or S2 stimulus. False alarms occurred on less than 1% of all trials. The average reaction time for target detection was 398 ms.

N170 to Mooney adaptors (S1)

Figure 2A shows grand-averaged ERP waveforms for our group of 16 DPs, elicited at lateral posterior electrodes P7 and P8 in response to adaptor stimuli (S1). ERPs are shown separately for upright and inverted Mooney faces and Mooney houses. N170 components were larger for upright Mooney faces relative to Mooney houses. Upright Mooney faces also elicited larger N170 components than inverted Mooney faces. An analysis of N170 mean amplitudes in response to upright Mooney faces and Mooney houses revealed a main effect of stimulus type, $F(1,15) = 37.98$, $p < .001$, $\eta_\rho^2 = .72$, confirming the generic face-sensitivity of the N170 component in response to Mooney stimuli in our group of individuals with DP. In fact, 15 of the 16 individuals tested showed numerically larger N170 amplitudes (averaged across P7 and P8) to upright Mooney faces as compared to Mooney houses. There was an interaction between stimulus type and hemisphere, $F(1,15) = 6.64$, $p = .021$, $\eta_\rho^2 = .31$, as the N170 amplitude enhancement to upright Mooney faces versus houses was larger over the right hemisphere. However, post-hoc t-tests confirmed that this effect was reliably present not only at right-hemisphere electrode P8, $t(15) = 5.37$ $p < .001$, but also at left-hemisphere electrode P8, $t(15) = 4.51$, $p < .001$. The scalp distribution of the N170 component to upright Mooney faces versus Mooney houses in the DP group in Figure 3 (left panel) shows the typical pattern during the N170 time window, with an occipito-temporal negativity (N170) accompanied by a more broadly distributed frontocentral vertex positive potential (VPP; Jeffreys, 1989). Upright Mooney faces also triggered larger N170 amplitudes than inverted Mooney faces, $F(1,15) = 23.83$, $p < .001$, $\eta_\rho^2 = .61$,

and this effect did not differ between hemispheres (F<1). Finally, N170 components to inverted Mooney faces were reliably larger relative to Mooney houses, F(1,15) = 27.82, p < .001, η_ρ^2 = .65. This difference was reliable over the right hemisphere, t(15) = 6.2, p < .001, but just failed to reach significance at left-hemisphere electrode P7, t(15) = 1.8, p = .081, and this was reflected by an interaction between stimulus type and hemisphere, F(1,15) = 12.91, p < .005, η_ρ^2 = .46.

N170 adaptation effects in response to naturalistic face test stimuli (S2)

Figure 2B shows grand-averaged ERPs for our group of 16 DPs, triggered at P7 and P8 to upright naturalistic face test stimuli. ERPs are shown separately for trials where test stimuli were preceded by upright Mooney faces, inverted Mooney faces or upright Mooney houses. There were systematic N170 adaptation effects, as N170 amplitudes to naturalistic test faces preceded by upright Mooney face adaptors were strongly reduced relative to N170 components to test faces preceded by Mooney houses. This difference between ERPs triggered by naturalistic test faces preceded by Mooney faces and Mooney houses was highly significant, F(1,15) = 27.16, p < .001, η_ρ^2 = .64. A comparison of N170 mean amplitudes to test faces (averaged across P7 and P8) on trials with upright Mooney face versus Mooney house adaptors for each individual DP revealed that all 16 participants tested showed N170 adaptation (an attenuation of N170 components following upright Mooney face adaptors). There was an interaction between adaptor type (upright Mooney faces versus Mooney houses) and hemisphere, as the N170 adaptation effect was larger over the right than the left hemisphere, F(1,15) = 17.36, p = .001, η_ρ^2 = .54. However, post-hoc t-tests revealed that this effect was reliably present over the right hemisphere, t(15) = 5.19, p < .001, as well as over the left hemispheres, t(15) = 3.11, p < .01. The scalp distribution of the N170 adaptation effect obtained for our group of 16 DPs is shown in Figure 3 (right panel). This map was computed by subtracting ERPs to test faces preceded by Mooney houses from ERPs to test faces preceded by upright Mooney faces. N170 adaptation (i.e., attenuation of N170 amplitudes on trials with upright Mooney face

adaptors) appears here as an increased posterior positivity that is larger over the right hemisphere and is accompanied by a frontocentral negativity (i.e., an adaptation-induced reduction of the VPP component). In addition, N170 adaptation was larger on trials with upright as compared to inverted Mooney face adaptors, $F(1,15) = 23.16$, $p < .001$, $\eta_p^2 = .61$. This difference was reliable at right-hemisphere electrode P8, $t(15) = 4.68$, $p < .001$, but only approached significance over the left hemisphere, $t(15) = 1.7$, $p = .11$. This was reflected by an interaction between adaptor type and hemisphere, $F(1,15) = 12.47$, $p = .003$, $\eta_p^2 = .61$.

Discussion

We employed a rapid neural adaptation procedure and measured ERP markers of perceptual face processing in a group of 16 individuals with developmental prosopagnosia to test whether in DP Mooney faces and naturalistic face images activate overlapping neural populations. Results were clear-cut, and suggest that individuals with DP are able to process Mooney faces in the same way as individuals with typical face recognition abilities. N170 components triggered in response to the three different types of adaptor stimuli (upright Mooney faces, inverted Mooney faces and Mooney houses) showed a qualitatively similar pattern in a group of DPs as a previous group of young non-prosopagnosic participants (see Figure 2A). N170 components were reliably larger for upright Mooney faces as compared to Mooney houses. This demonstrates that the generic face-sensitivity of the N170 is preserved in DP, not only for naturalistic face stimuli (Towler et al., 2012), but also for Mooney faces. The observation that N170 components to upright Mooney faces were larger than N170 components to inverted Mooney faces shows that the N170 component in DPs remains sensitive to holistic information about the presence of a face in a canonical orientation, even in the absence of low-level features that could be independently recognized as part of a face. It should be

noted that no such difference between N170 components between upright and inverted face adaptors was observed in our previous study with unimpaired participants (Eimer et al., 2011; see Figure 1B). The factor responsible for this apparent difference between studies appears to be the choice of reference electrodes for EEG analysis. When the data from the previous study (Eimer et al., 2011) were transformed to the same common average reference as the DP data in the present study, the difference between upright and inverted Mooney faces also emerged for unimpaired participants. Some earlier ERP studies found a reduction of N170 amplitudes for inverted versus upright Mooney faces in unimpaired participants (Latinus & Taylor, 2005; George et al., 2005) while others did not (Latinus & Taylor, 2006; Eimer et al., 2011). Previous studies that have used a common average reference have tended to at least show a numerical difference between upright and inverted Mooney faces on N170 amplitudes (Latinus & Taylor, 2005; 2006; for similar results with ambiguous face paintings also see: Caharel, et al., 2013) while the one study that used an average ears reference found no differences (Eimer et al., 2011). In summary, these apparent differences in N170 amplitudes between upright and inverted Mooney faces for DPs in the present study are unlikely to reflect a deviation from normal face processing in DP.

This conclusion was further confirmed by the adaptation effects observed for N170 components in response to naturalistic test face images (see Figure 2B). N170 amplitudes were reliably reduced in the DP group on trials where these test faces were preceded by upright Mooney face adaptors relative to trials with Mooney house adaptors, and this N170 adaptation effect was very similar to the effect observed for unimpaired participants. N170 adaptation was stronger on trials with upright as compared to inverted Mooney face adaptors, in line with the assumption that there is a strong overlap in the face-sensitive neural populations activated by upright Mooney faces and upright naturalistic faces, and that this overlap is much reduced when inverted Mooney face adaptors are presented instead.

The assumption that naturalistic faces and Mooney faces activate overlapping face-sensitive neural populations, and that this is the case also in individuals with DP, was further supported by an additional comparison between the face-selectivity of N170 components in response to naturalistic stimuli from our previous study with the same DP participants (Towler et al., 2012) and the face-selectivity of the N170 to Mooney images reported here. In both studies, participants with DP showed robust differences between N170 amplitudes triggered by upright faces and houses. N170 amplitude differences naturalistic faces versus houses and Mooney faces versus houses were closely correlated ($r = .69$, $p < .005$), such that DPs with larger N170 amplitude differences between naturalistic faces and houses also showed larger differences between Mooney faces and houses. Despite the fact that the naturalistic and Mooney images were physically very different, the significant correlation of the N170 face sensitivity between these two types of stimuli suggests that the underlying face-selective visual processes are functionally similar. As mentioned earlier, the absence of differences in face-selective N170 amplitude enhancements between DPs and age-matched controls (Towler et al., 2012) suggest that these processes are generally unimpaired in DP.

Overall, our findings show that some basic aspects of holistic face processing at the categorical level are not impaired in developmental prosopagnosia. They show conclusively that individuals with DP can rapidly access holistic information about the presence of face-like configurations that is provided by Mooney face stimuli. The critical property of these two-tone images is that they do not contain local features that would be recognizable as part of a face independently of the overall holistic pattern of these stimuli. In spite of this fact, N170 components remained sensitive to the difference between face and non-face images in our group of DPs. Furthermore, the presence of systematic N170 adaptation effects demonstrated that Mooney faces and naturalistic faces activate shared neural mechanisms in this group. As described above, our previous study (Towler et al., 2012) has shown that the generic face-sensitivity of the N170 component (i.e., larger N170 amplitudes to naturalistic images of faces versus houses) was preserved in the same individuals with DP. As the N170 is known to be sensitive to individual facial features even when these features are presented in

isolation (Bentin et al., 1996) this effect could in principle exclusively reflect the part-based processing of facial features at the local level, and not any holistic aspects of face processing in DP. The current observation that the processing of Mooney faces is essentially normal in the DP group shows that this is not the case, and that sensitivity to holistic face information remains intact in DP.

Our findings are also consistent with a previous study which showed no behavioural impairment in the detection of upright Mooney faces in a group of eight DPs (Le Grand et al., 2006). Along similar lines, the detection of Mooney faces was also normal in patients with congenital cataracts (Mondloch et al., 2003), who are known to have face recognition impairments, including difficulties in the holistic processing of individual faces (Le Grand et al., 2001; 2004). Our results are also in line with observations from PS, a patient with acquired prosopagnosia and severe face recognition impairments, who was able to successfully detect Mooney faces, and showed normal face-selective responses in her intact FFA and a stronger response to upright as compared to inverted Mooney faces in this region (Rossion et al., 2010). Most DPs show face-selective FFA activation in fMRI studies and normal face-sensitivity of the N170 component (e.g. Furl et al., 2011; Towler et al, 2012). In line with our current findings, these previous observations suggest that face processing in DP retains some sensitivity to the holistic structure of faces, and that this information contributes to the differential neural processing of faces versus non-faces that has been demonstrated with fMRI and ERP measures.

How does our conclusion that Mooney faces are processed normally in developmental prosopagnosia relate to our previous finding that N170 face inversion effects are atypical in DP (Towler et al., 2012)? In this study, the same 16 participants who showed typical N170 responses to upright and inverted Mooney faces did not show the usual N170 amplitude enhancement for inverted as compared to upright naturalistic face images. The increase of N170 amplitudes in response to inverted faces has been attributed to the recruitment of additional face-unspecific object-selective neural populations by these faces, or to an enhanced contribution from face-

selective neurons (Rosburg et al., 2010; Sadeh & Yovel, 2010). The absence of inversion-induced N170 amplitude enhancements in individuals with DP suggests that face processing was not selectively tuned to the canonical upright orientation of naturalistic faces in this group. If both upright and inverted faces recruit not just face-selective neurons, but also additional object-selective neurons in individuals with DP, there should be no systematic N170 amplitude differences between these two types of stimuli, as was indeed observed (Towler et al., 2012). In contrast to inverted naturalistic faces, inverted Mooney faces are usually not perceived as meaningful objects, and will therefore not trigger strong responses from either object or face-selective neurons. The reduction in N170 amplitude for inverted Mooney faces is therefore likely to reflect a reduction in the response of face-selective cells when holistic cues about the presence of a face are weak or absent (see also Kanwisher et al., 1998, for an activity decrease in the fusiform face area (FFA) in response to inverted Mooney faces). The fact that DPs show the typical N170 amplitude reduction for inverted as compared to upright Mooney faces, and a corresponding pattern of N170 adaptation effects, shows that when additional contributions from object-selective neuronal populations are excluded, face processing in DP remains sensitive to holistic information about the presence of a face that is provided by upright Mooney face images.

Another possibility is that N170 face inversion effects for naturalistic stimuli originate from a failure to successfully integrate specific facial features (e.g. the eyes) within the context of the whole face arrangement in inverted faces as compared to upright faces (for reductions of N170 face inversion effects when the eyes are artificially removed from the face, see: Kloth, Itier & Schweinberger, 2013; Magnuski & Gola, 2013). Mooney faces do not contain explicitly recognisable face parts outside of the face context and so this integration process does not occur. For this reason, face inversion does not produce the characteristic N170 amplitude enhancements and latency delays. Normal N170 modulations for upright Mooney faces as compared to Mooney houses and inverted Mooney faces suggest that the detection of holistic cues to face presence operate normally in DP. On this account, atypical N170 inversion effects for naturalistic images in the same DP participants suggest that it

may be the early integration of local face feature cues and their surrounding context that is impaired in DP (for behavioural evidence, see: DeGutis et al., 2012; Kimchi et al., 2012). Put differently, individuals with DP may be sensitive to face cues in particular spatial frequency bands. Mooney faces appear to contain low spatial frequency information (e.g. see Figure 1B) and one possibility is that DPs are able to extract low spatial frequency information about basic face shape. With this in mind, it is interesting to note that more fine-grained information which is useful for recognition of individual identities is contained mainly in middle spatial frequency bands (e.g. Näsänen, 1999; Tanskanen et al, 2005).

It has previously been argued that there are two types of prosopagnosic deficits (De Renzi et al., 1991) – impairments in face perception (apperceptive prosopagnosia) and impairments in face memory (associative prosopagnosia). Some individuals with prosopagnosia have demonstrated difficulties in matching faces in perceptual tasks with low memory demands, while others seem to perform normally at this task (De Renzi et al., 1991; Duchaine et al., 2007). Those individuals who perform normally at perceptual tasks appear to have associative deficits in matching visual representations of faces with stored memory representations of known faces, or impaired links between visual representations and the semantic system (see Eimer et al., 2012, for evidence of disconnection between visual and post-perceptual processing stages in DP). However, our current and previous findings suggest that a simple apperceptive-associative dichotomy may be too crude to fully capture the kinds of face processing deficits in developmental prosopagnosia. The present study shows that the category-level processing of Mooney faces that is based on holistic information about the presence of face-like configurations in the absence of local cues from individual facial features is essentially normal in DP. But this result should not be taken to imply that face perception is generally intact in individuals with DP. Many of the DPs in this study have some level of difficulty with a standardised face perception task (CFPT), and showed reduced inversion effects for identity judgements as compared to normal controls (see Table 1). Furthermore, these very same participants showed atypical N170 inversion effects to naturalistic face stimuli (Towler et al., 2012).

It is possible that the processing of faces versus non-faces at the basic category level is normal in DP, and that deficits emerge at subsequent stages of face perception, such as the analysis of subtle differences in relationships between facial features, which are necessary for distinguishing between individual faces (e.g. Le Grand et al. 2006; Yovel & Duchaine, 2006). It has been argued that stimulus categorisation and individuation have opposing computational demands (Tsao & Livingstone, 2008): Categorisation requires detecting stimulus properties which are shared across different exemplars to include them in a particular set. By contrast, individuation is based on the detection of more subtle differences between homogenous exemplars from the same category, in order to identify particular exemplars from within this category. The current results suggest that individuals with developmental prosopagnosia can utilize first-order configural information at a holistic processing level for basic discriminations between face and non-face objects. However, face recognition impairments in DP could still reflect perceptual problems with analysis of fine-grained details present in faces or their sensitivity to contextual cues that alter the appearance of individual features and are important for individual face recognition.

Participant	Age	Sex	FFT (%)	CFMT z	CFPT upr z	CFPT inv z	ONT z
MC	41	M	24.6	-1.38	-1.54	-1.62	-2.46
EW	32	F	13.3	-2.64	0.92	0.2	-3.43
CM	29	M	20.7	-4.29	-3.1	-2.89	-14.34
NE	31	F	33.3	-2.77	-1.06	-1.62	-4.17
JA	46	F	43.6	-2.64	-0.92	-0.49	-3.35
AH	48	F	60.0	-1.76	-1.06	-0.63	-2.04
AM	28	F	46.4	-2.64	-1.74	-0.49	-2.88
SW	28	F	22.0	-2.64	-1.74	-1.05	-2.95
KS	29	F	15.1	-2.9	-0.92	-1.05	-9.03
SC	22	F	44.7	-2.64	-0.51	0.08	-4.15
JL	67	F	40.0	-1.76	-2.29	-0.49	-6.27
SN	54	F	52.5	-2.26	-2.15	0.36	0.42
MZ	48	F	53.6	-2.52	-1.33	0.22	-6.47
CP	39	F	34.7	-2.64	-0.92	1.21	-1.11
RL	49	M	19.6	-3.65	-1.88	-0.77	-5.87
MP	49	M	36.8	-2.9	-1.33	0.64	-4.42

Table 1. Details of the 16 DPs who participated in this experiment, and their performance on different behavioural tests of face processing. For the Famous Face Test (FFT), the percentage of correctly recognized faces is listed (recognition rate for unimpaired participants is above 90%; Garrido et al., 2008). For the Cambridge Face Memory Test (CMFT), the Cambridge Face Perception Test (CFPT) with upright and inverted faces (upr/inv), and for the Old-New Test (ONT), z-scores of each individual's performance are listed (see text for details).

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Figure Legends

Figure 1

(A) Illustration of the trial structure and timing of the adaptor and test stimuli used in the rapid adaptation paradigm. (B) Results from our previous study (Eimer, 2011). Grand averaged ERPs for neurotypical participants elicited at lateral right hemisphere electrode P8 in response to S1 stimuli (adaptors) in the 300ms interval after stimulus onset. ERPs are shown for upright Mooney faces (black lines), inverted Mooney faces (light grey lines) and Mooney houses (dark grey lines). (C) Grand-averaged ERPs elicited at lateral right hemisphere electrode P8 in response to S2 test stimuli (upright naturalistic faces) in the 300 ms interval after S2 onset, separately for trials where these faces were preceded by upright Mooney face adaptors (black lines), inverted Mooney face adaptors (grey lines), and Mooney house adaptors (dashed lines).

Figure 2

(A) Grand-averaged ERPs for DP participants elicited at lateral posterior electrodes P7/P8 in response to S1 stimuli (adaptors) in the 300 ms interval after stimulus onset, shown separately for upright Mooney faces (black lines), inverted Mooney faces (light grey lines), and Mooney houses (dark grey lines). (B) Grand-averaged ERPs elicited at electrodes P7/P8 in response to S2 test stimuli (upright naturalistic faces) in the 300 ms interval after S2 onset, separately for trials where these faces were preceded by upright Mooney face adaptors (black lines), inverted Mooney face adaptors (grey lines), and Mooney house adaptors (dashed lines).

Figure 3.

Left panel: Topographic maps showing the scalp distribution of N170 components to upright Mooney face adaptors versus Mooney house adaptors for the DP participants. Difference potentials

were obtained in the N170 time window (150-200 ms after stimulus onset) by subtracting ERPs to Mooney houses from ERPs to Mooney upright faces. Larger negative amplitudes for faces (N170 component) are shown in blue, larger positive amplitudes for faces (VPP component) are shown in red. Right panel: Topographic maps showing the scalp distribution of N170 adaptation effects for upright face test stimuli on trials with Mooney faces versus houses. Maps were obtained in the N170 time window (150-200 ms after stimulus onset) by subtracting ERPs to upright naturalistic faces preceded by Mooney houses from naturalistic faces preceded by upright Mooney faces (left). N170 adaptation effects (i.e., smaller N170 amplitudes on trials with Mooney face adaptors) are shown in red.

Figure 1

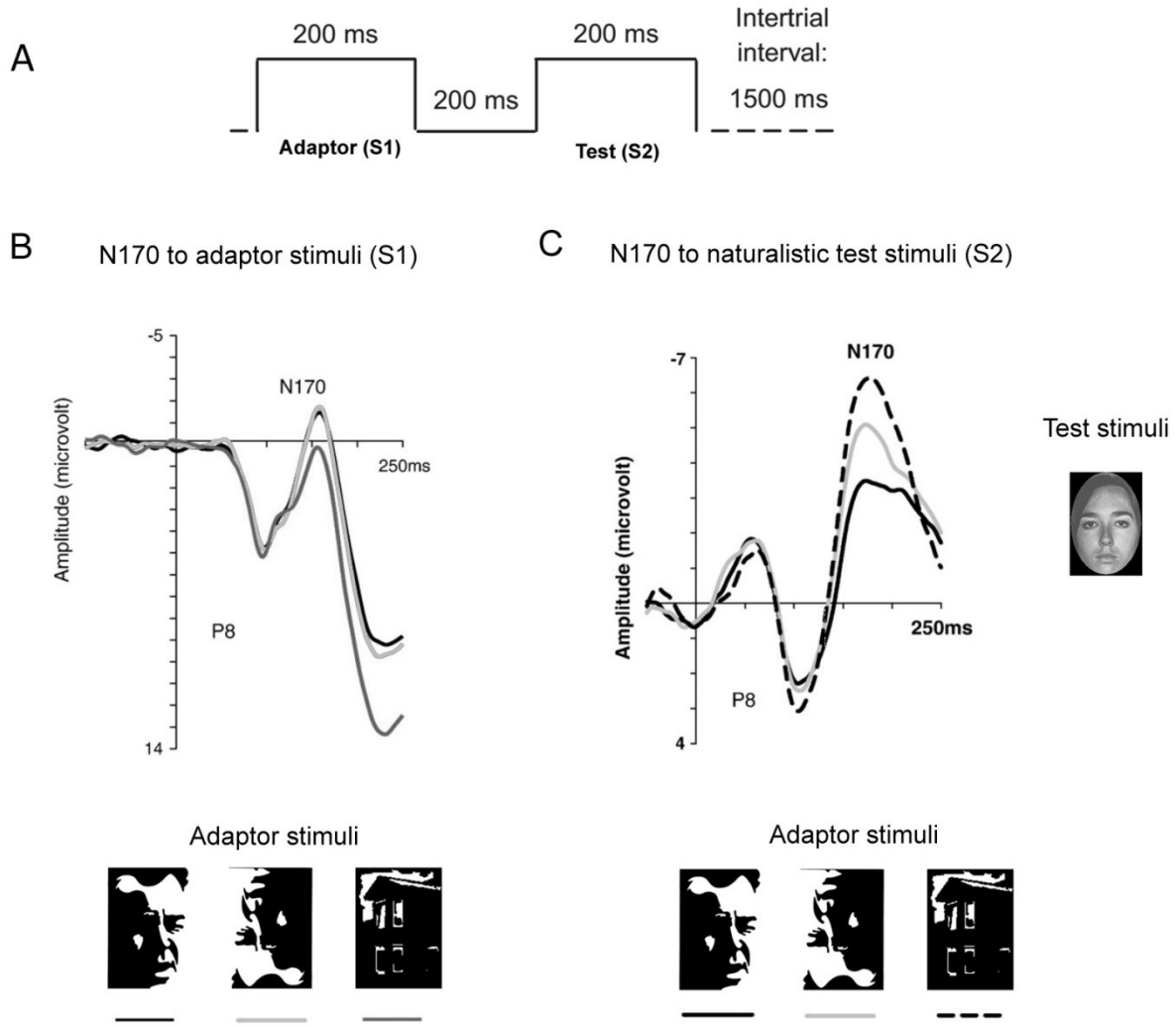

A
200 ms
200 ms
Intertrial interval:
200 ms
1500 ms
Adaptor (S1)
Test (S2)
B
N170 to adaptor stimuli (S1)
C
N170 to naturalistic test stimuli (S2)
-5
N170
250ms
Amplitude (microvolt)
P8
14
-7
N170
Amplitude (microvolt)
250ms
P8
4
Test stimuli
Adaptor stimuli
Adaptor stimuli

Figure 2

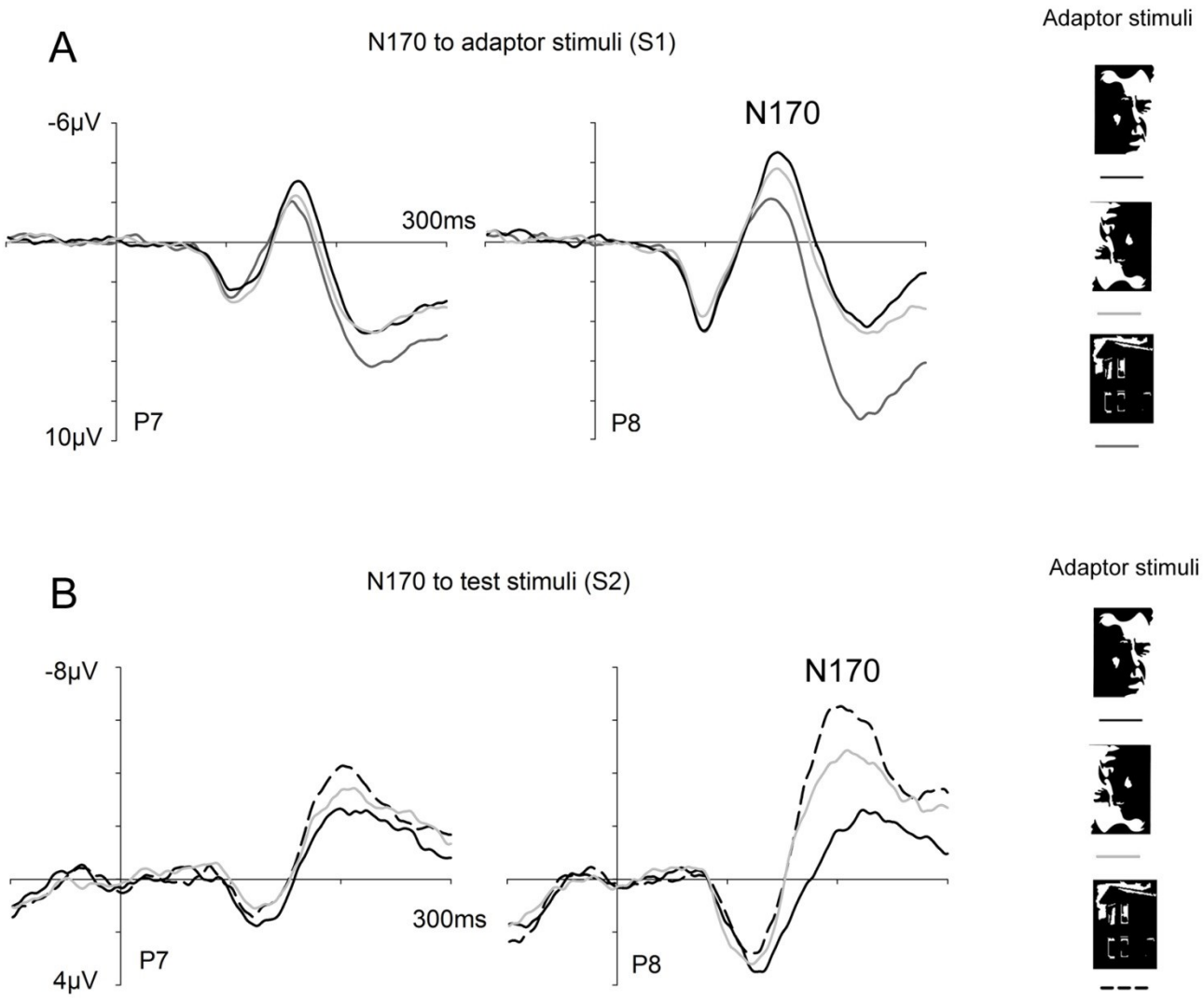
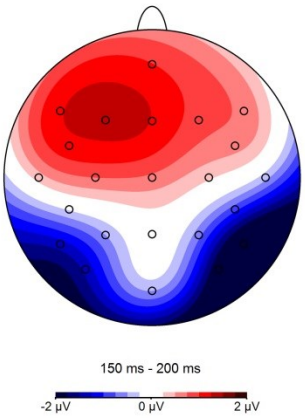
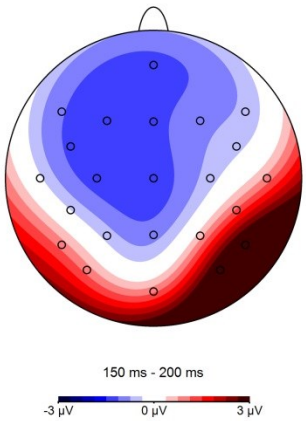

A
N170 to adaptor stimuli (S1)
-6μV
10μV
300ms
P7
P8
N170
Adaptor stimuli
B
N170 to test stimuli (S2)
-8μV
4μV
300ms
P7
P8
N170
Adaptor stimuli

Figure 3 N170 scalp topographies

S1: Upright Mooney Face - Mooney House



S2: Preceded by Upright Mooney Face - Mooney House