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Probing the face-space of individuals with prosopagnosia

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ABSTRACT

A useful framework for understanding the mental representation of facial identity is face-space (Valentine, 1991), a multi-dimensional cognitive map in which individual faces are coded relative to the average of previously encountered faces, and in which the distance among faces represents their perceived similarity. We examined whether individuals with prosopagnosia, a disorder characterized by an inability to recognize familiar faces despite normal visual acuity and intellectual abilities, evince behavior consistent with this underlying representational schema. To do so, we compared the performance of 6 individuals with congenital prosopagnosia (CP), with a group of age- and gender-matched control participants in a series of experiments involving judgments of facial identity. We used digital images of male and female faces and morphed them to varying degrees relative to an average face, to create caricatures, anti-caricatures, and anti-faces (i.e. faces of the opposite identity). Across 5 behavioral tasks, CP individuals' performance was similar to that of the control group and consistent with the face-space framework. As a test of the sensitivity of our measures in revealing face processing abnormalities, we also tested a single acquired prosopagnosic (AP) individual, whose performance on the same tasks deviated significantly from the control and CP groups. The findings suggest that, despite an inability to recognize individual identities, CPs perceive faces in a manner consistent with norm-based coding of facial identity, although their representation is likely supported by a feature-based strategy. We suggest that the apparently normal posterior cortical regions, including the fusiform face area, serve as the neural substrate for at least a coarse, feature-based face-space map in CP and that their face recognition impairment arises from the disconnection between these regions and more anterior cortical sites.

Face-space is a useful conceptual framework for understanding how we represent facial identity (Valentine, 1991). Face-space is a multi-dimensional space centered on the average of previously experienced faces at its origin, and with individual identities represented as unique vectors from the origin. The distance from the origin represents the distinctiveness of a face because, by definition, typical faces should look more like the average face and, therefore, be located closer to the average. The direction from the origin represents *how* the face deviates from average, that is, along what particular facial dimension the face is distinct. These facial dimensions are ill-defined, as adults appear to use an amalgam of facial features that cannot be easily verbalized when making facial identity judgments (Nishimura, Maurer, & Gao, 2009). Sensitivity to both individual facial features as well as combinations of features has also been reported recently in face-selective neurons of the macaque temporal lobe (Freiwald, Tsao, & Livingstone, 2009). Nonetheless, such a coding scheme results in a face-space layout such that the distance between two faces represents the perceived similarity of those faces (the smaller the distance, the more similar the faces), and many faces cluster around the average whereas few faces sparsely occupy the periphery.

Face-space is a powerful and robust framework for understanding the underlying coding of facial identity and it has been adopted in many recent studies that explore the psychological and neural substrate of face processing. For one, it can account successfully for the apparently paradoxical effect of distinctiveness on face detection versus identification. The paradoxical finding is that adults demonstrate faster classification of *typical* faces as faces but faster individual recognition of *distinctive* faces (e.g., Johnston & Ellis, 1995; Lee, Byatt, & Rhodes, 2000; Rhodes, Byatt, Tremewan, & Kennedy, 1997; Valentine, 1991; Valentine & Bruce, 1986). According to the face-space framework, viewing a face activates an area of face-space that corresponds to the diagnostic dimensional values of that face. As such, distinctive faces will be better *recognized* because they are in a low-density region, making it less likely that neighboring faces will be erroneously activated. However, typical faces will be better detected or classified as a face, because, in a high-density region, activation may encompass several faces, lead-

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Table 1
Performance of typical adults and individuals with prosopagnosia on a Famous Faces Questionnaire and a Face Discrimination Task (all results except for performance of MN from Behrmann et al., 2005).

Participant	Accuracy on famous face questionnaire	Median RT on upright face discrimination task	Median RT on inverted face discrimination task
Controls	86.5%(95% CI = ±10.4%)	2592 ms(95% CI = ±597 ms)	3549 ms(95% CI = ±962 ms)
CP mean	47.6%	4145 ms	3805 ms
IM	33.5%	4082 ms	5210 ms
MT	62.5%	8386 ms	7039 ms
WA	50%	1043 ms	5210 ms
TD	46.7%	1635 ms	1817 ms
IT	33.9%	7846 ms	5573 ms
MN	58.9%	1880 ms	1567 ms
AP	17.0%	5934 ms	5785 ms

ing to a stronger signal indicating that the stimulus is a face. The face-space framework also predicts that caricaturing a face (i.e., enhancing some distinctive facial feature, like Jay Leno's lower jaw), will enhance recognition because caricaturing moves the face away from the average and into an area of lower spatial density, and this is indeed true of adults' performance (e.g., Rhodes, Brennan, & Carey, 1987).

The current study examines the nature of "face-space" in individuals with prosopagnosia, a disorder in which face recognition is impaired. Specifically, prosopagnosia is characterized by the inability to recognize familiar faces despite intact low-level visual functions and general cognitive abilities (e.g., Behrmann & Avidan, 2005; Dobel, Bolte, Aicher, & Schweinberger, 2007). Because the condition appears to be associated specifically with recognizing individual faces, we hypothesized that the mental representation of faces in individuals with prosopagnosia may not adhere to the face-space framework. In congenital prosopagnosia (CP), where the condition has been present presumably since birth, it is unclear to what extent the mental representation of faces has an underlying structure, and/or to what extent compensatory mechanisms have developed for making facial identity judgments. The goal of this study is to explore for the first time whether the underlying coding of faces in CP individuals adheres to principles of face-space. In addition, we include a single acquired prosopagnosic (AP) individual in our sample whose performance provides a test for the sensitivity of our measures to reveal abnormalities in face processing. We compare the ability of the prosopagnosic individuals and matched controls to make decisions about morphed faces that are either more or less like the average face, as a means of tapping into the representation mediating their face perception. The nature and extent to which face-space is perturbed will shed important light on our understanding of the mechanisms giving rise to the recognition impairment in CPs.

We conducted three separate experiments to examine the mental representation of facial identity in individuals with prosopagnosia. In Experiment 1, to assess whether facial identity appears to be coded relative to the average or norm, we examined facial identity aftereffects (e.g., Leopold, O'Toole, Vetter, & Blantz, 2001). To assess the spatial density of the individuals' "face-space", we examined the effect of caricaturing on face perception (Experiment 2). Finally, to assess the underlying dimensions representing "face-space", we collected prosopagnosics' similarity ratings of pairs of faces and conducted multi-dimensional scaling analysis (Experiment 3).

1. General methods

1.1. Participants

Participants were 6 individuals with CP (age range 20–70 years), one individual with AP (age 34 years) resulting from a brain injury following a motor vehicle accident, and 14 typical participants matched to each of the prosopagnosics by age (±5 years), race, and gender (two per individual). Many of the CP individuals have participated previously in our studies, and details of their behavioral profiles can be found in Table 1 and in previous published reports (e.g., Avidan, Thomas, & Behrmann, 2008; Behrmann & Avidan, 2005). The AP individual, SM, has also participated in previous studies (Behrmann & Kimchi, 2003; Behrmann, Marotta, Gauthier, Tarr, & McKeeff, 2005; Behrmann, Peterson, Moscovitch, & Suzuki, 2006; Behrmann & Williams, 2007). Briefly, SM sustained a lesion centered on the right inferotemporal lobe, and, despite good recovery from the accident (aside from a mild left hemiparesis), his major symptom is a profound impairment in face recognition. He also shows evidence of object agnosia, although this is not as pronounced as the prosopagnosia (Behrmann & Williams, 2007; Gauthier, Behrmann, & Tarr, 1999).

The control participants were recruited from the community. Additionally, the performance of this matched control group was compared to a group of approximately 20 university-aged participants (per experiment), to assess whether our control group's performance differed from previously established norms for adults because there is a wide age range in our matched control group. The expectation is that there would be no difference between them but this remained to be established.

1.2. Analysis

For each task, we first conducted ANOVAs to compare the performance between our matched control group and previously collected adult norms. Upon verifying that the performance between the two control groups did not differ, we proceeded to compare the matched control group and the CP group using ANOVAs. In addition, each CP and AP individual's score was compared to the matched control group, using Crawford's modified *t*-test for single cases (Crawford & Garthwaite, 2002). This last measure is becoming increasingly popular as a robust method of assessing whether a single individual's score diverges significantly from those of a control group.

2. Experiment 1: Identity aftereffects

A key characteristic of the face-space framework is that individual faces are coded relative to an average (i.e., norm-based coding). Recent adaptation paradigms provide supporting evidence that face-space is centered on the average face (Rhodes et al., 1987; Rhodes, Jeffery, Watson, Clifford, & Nakayama, 2003; Valentine, 1991), and that individual identities are coded as deviations from the average or norm (Leopold et al., 2001; Rhodes & Jeffery, 2006; Webster & MacLin, 1999). The face identity aftereffect is demonstrated by creating pairs of "opposite" faces relative to the average. For example, if Dan has a large forehead (relative to average), "anti-Dan" is created to have a proportionately smaller-than-average forehead, and similarly all other facial characteristics in anti-Dan are morphed simultaneously to be opposite of Dan relative to

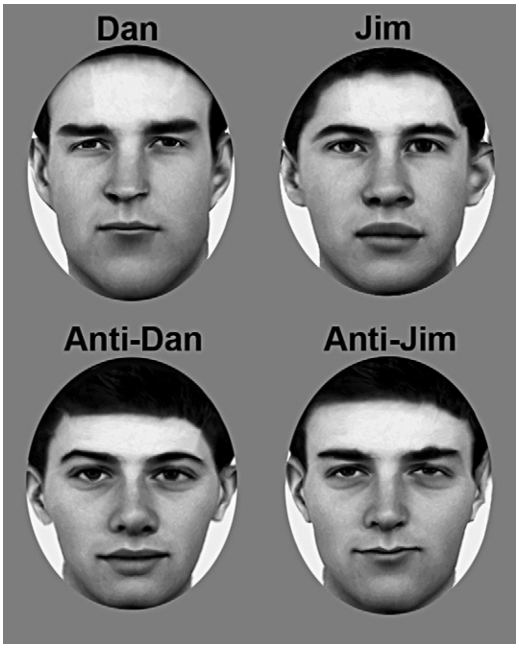

Fig. 1. Test stimuli (100% identity strength) and adapting stimuli (80% anti-faces) used in examining facial identity aftereffects (for details of stimuli see Rhodes & Jeffery, 2006).

the average. In typical children and adults, adapting to anti-Dan temporarily shifts the perceived identity of an identity-neutral (e.g. average) face towards Dan (e.g., Anderson & Wilson, 2005; Nishimura, Maurer, Jeffery, Pellicano, & Rhodes, 2008; Rhodes & Jeffery, 2006), and such aftereffects are consistent with a model of norm-based coding of facial identity (for a review, see Tsao & Freiwald, 2006).

2.1. Methods

2.1.1. Stimuli

The details of the stimuli and method have been published previously (Nishimura et al., 2008; Pellicano, Jeffery, Burr, & Rhodes, 2007; Rhodes & Jeffery, 2006). Briefly, 187 landmarks were defined on each of 20 grey-scale digitized male faces and then averaged to create an “average face”. Two out of the 20 identities used in previous studies, Dan and Jim, were chosen as test stimuli (Fig. 1). The faces of Dan and Jim were systematically morphed to be more like the average face, resulting in five identity strengths for testing (0, 20, 40, 60, and 80% of the original identities) and 3 identity strengths for training (40, 60, and 100% of the original identities). In addition, 80% anti-faces (anti-Dan and anti-Jim, see Fig. 1) were created by morphing the faces away from the average face in the direction opposite to the original faces (for details see Leopold et al., 2001; Rhodes & Jeffery, 2006).

2.1.2. Procedure

The procedure was modeled after a paradigm used previously with children and adults (Nishimura et al., 2008; Pellicano et al., 2007). Briefly, participants were trained to identify correctly the 100% Dan and Jim stimuli, referred to as the Team Captains, and their weaker 40 and 60% identity morphs, referred to as the “brothers” of Dan and Jim, forming Team Dan and Team Jim. Training continued for each participant until he/she correctly identified the 40 and 60% morphs as belonging to Team Dan or Jim in at least 4 out of the 5 criterion trials, before proceeding to the testing phase. In the testing phase, there were 3 blocks: pre-adaptation baseline, adaptation, and post-adaptation baseline (identical to pre-adaptation baseline). In the pre- and post-adaptation baseline blocks, participants viewed a single face shown for 400 ms, and indicated whether the face belonged to “Team Dan” or “Team Jim” by using one of two key presses. Each identity strength (0, 20, 40, 60, and 80%) of Dan and Jim was shown 6 times. The adaptation block was identical to the baseline block except that, prior to the test face, an adapting face was shown for 5 s. For half of the trials (30 trials), the adapting face was anti-Dan and for the other half (30 trials), the adapting face was anti-Jim. The trials were presented in random order across participants.

2.1.3. Initial analyses

We first compared performance between pre- and post-adaptation baseline (i.e. *time of test*, a within-subjects variable) to examine any long-lasting adaptation aftereffects. A repeated measure ANOVA on the performance of the matched control group versus the CP individuals (between-subject variable) at each *identity strength* tested (within-subjects variable, 5 levels: 0, 20, 40, 60, and 80%) revealed no main effect of *group*, $F(1, 18) = 0.50$, $p = .49$, indicating that the two groups learned the stimuli equally well. There was also no main effect of *time of test* (pre- vs. post-adaptation), $F(1, 18) = 0.06$, $p = 0.82$, and no significant interactions of *time of test* with *group* ($p = .97$), *identity strength* ($p = .81$), and no 3-way interaction of *time of test* × *group* × *identity strength* ($p = .42$). Therefore, performance was collapsed across pre- and post-adaptation baseline into a single variable Baseline for all subsequent analyses.

For each participant, we computed the proportion of “Team Dan” responses for each test face, separately for Baseline trials, Adaptation trials with anti-Dan, and Adaptation trials with anti-Jim. We conducted nonlinear regression curve fitting with a sigmoidal equation (with variable slope) using Prism software (version 4.0a) to quantify the point of subjective equality (PSE; see Fig. 2). The PSE represents the identity strength of the stimulus at which point observers were equally likely to respond “Team Dan” and “Team Jim”. Without any adapting stimulus (i.e. baseline condition), we would predict the PSE to be equal to zero (0% identity strength = the average face). For trials in which observers adapted to anti-Dan, the PSE should shift, relative to Baseline, towards the “Jim” identity, because a “Dan” bias in perceived identity means that for any given face, less “Dan-ness” is required for a “Team Dan” response. Conversely, for trials in which observers adapted to anti-Jim, the PSE should shift towards the “Dan” identity, because more “Dan-ness” is required for a “Team Dan” response.

2.2. Results

The PSEs of the matched control group and CP individuals on Baseline trials and Adaptation trials with anti-Dan and anti-Jim stimuli are shown in Fig. 2 (group and individual plots). A repeated measure ANOVA on the PSEs derived for each participant for each of the three conditions (Baseline, anti-Dan Adaptation, anti-Jim Adaptation) revealed no main effect of *group*, $F(1, 18) = 0.01$, $p = 0.93$, and no significant *group* × *condition* interaction, $F(2, 36) = 1.41$, $p = 0.26$, which suggests that CP individuals were showing identity aftereffects in a manner similar to the matched control group. As expected, there was a main effect of *condition*, $F(2, 36) = 5.10$, $p < 0.05$. Post hoc analyses revealed that the PSE was significantly less than Baseline after adapting to anti-Dan, $t(19) = 3.06$, $p < 0.01$, a result that reveals an identity aftereffect reflecting a bias to respond “Team Dan” after adapting to anti-Dan. However, the identity aftereffect, after adapting to anti-Jim, failed to reach statistical significance, $t(19) = -1.24$, $p = 0.23$, which was unexpected, but the shift in PSE was in the expected direction and, most importantly, was similar for both CP and control groups.

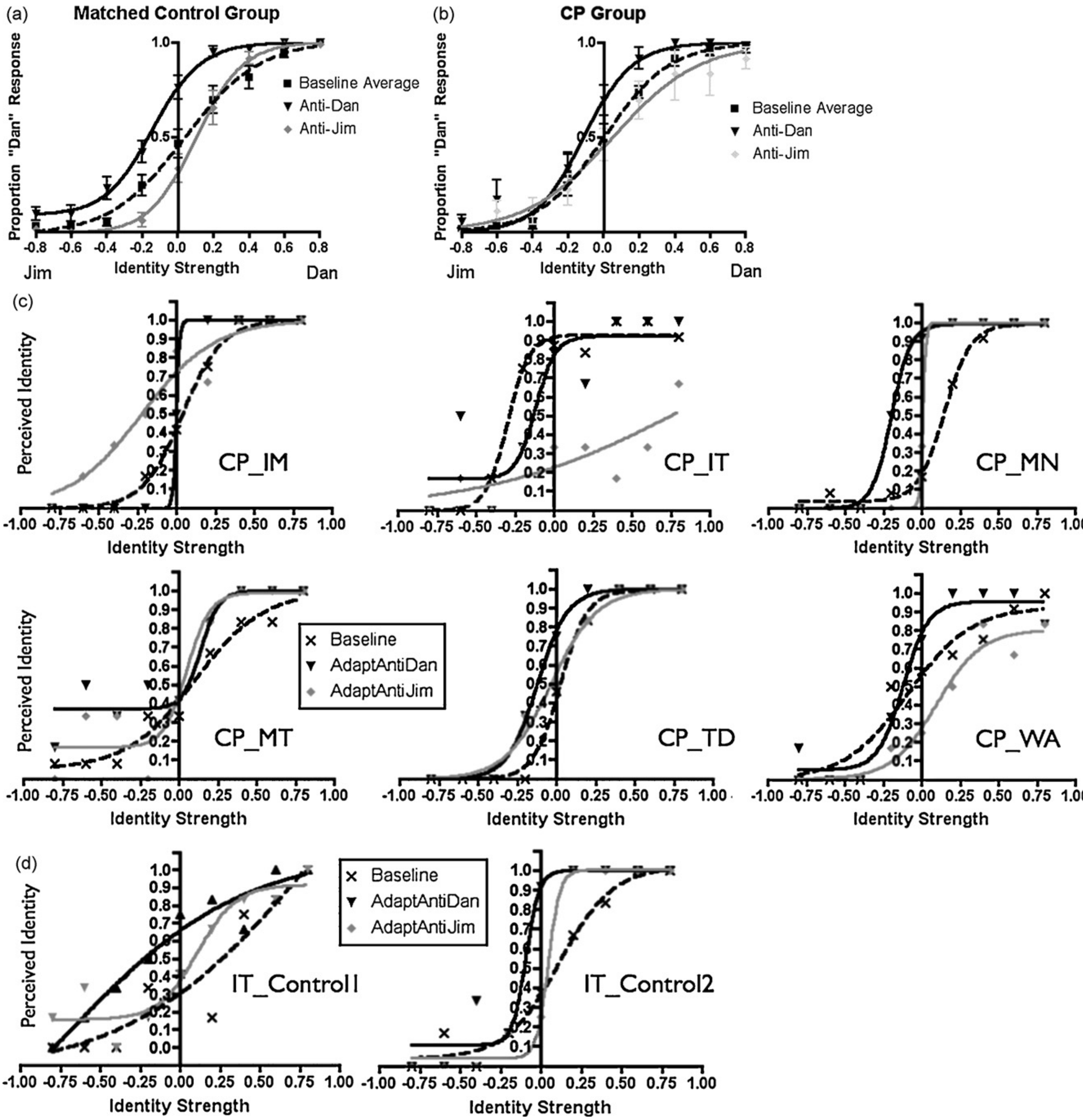

Fig. 2. The proportion of "Team Dan" responses as a function of identity strength during Baseline and Adaptation trials (adapting to anti-Dan and anti-Jim shown separately) for (a) matched control group ($n = 14$), (b) CP group ($n = 6$), (c) individual CPs, and (d) two control participants matched to IT. The point of subjective equality (PSE) is the identity strength at which the curve is equal to 0.5 on the y-axis, where observers are equally likely to respond "Team Dan" and "Team Jim".

To assess individual performance of the CPs, we conducted Crawford's modified t-test on the size of the identity aftereffect in anti-Dan trials only for each CP individual using the mean of the matched control group, and for each control participant using the mean of the remaining control participants. IM showed significantly smaller aftereffects than controls (Fig. 3). The findings suggest that the CP individuals, except IM, showed identity aftereffects that were similar to the matched control group.[1]

As can be seen in Fig. 2c and d, not every individual showed the expected pattern of identity aftereffects, but each participant's data could be fit with a sigmoidal curve. In contrast, the AP individual's performance (see Fig. 4) deviated significantly from the response pattern of the matched control group and the CP group, such that a sigmoidal curve could not be fit to the data in any of the conditions. Although the AP individual appears to have learned transiently the Dan and Jim identities well enough to pass our training cri-

[1] Alternatively, we could assess individual performance using the average shift in PSE from both anti-Dan and anti-Jim trials combined. This analysis also did not reveal any group differences. One CP individual (IM) and one control participant showed significantly smaller aftereffects and one CP individual (IT) and one control participant showed significantly larger aftereffects than the (rest of the) control group.

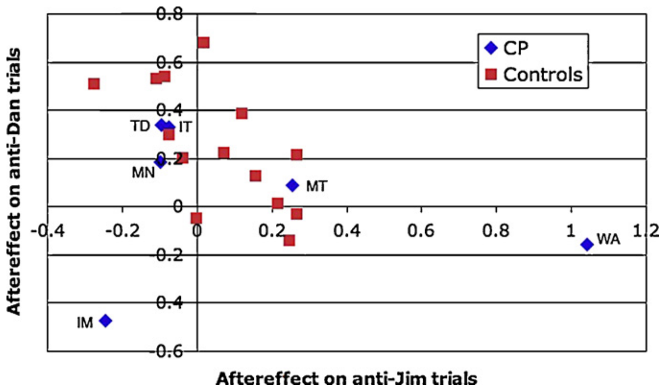

Fig. 3. Mean identity aftereffect (anti-Dan trials only) for the matched control group (+1 SE) and CP individuals.

terion, performance in the Baseline condition (without feedback) reveals that the representation was likely unstable and short-lived, as his response pattern does not correspond in a systematic fashion to changes in identity strength, and his response profile is rather erratic and random.

2.3. Discussion

One of the key characteristics of the face-space framework is norm-based coding: coding of individual facial identities relative to the average of previously encountered faces. To assess norm-based coding in individuals with prosopagnosia, in this study, we examined whether individuals with prosopagnosia would demonstrate facial identity aftereffects. Previous research with adults have shown facial aftereffects in the direction opposite to the adapting face, relative to an averaged face (e.g., Leopold et al., 2001; Rhodes & Jeffery, 2006; Tsao & Freiwald, 2006; Watson & Clifford, 2003; Webster & MacLin, 1999), as well as a lack of such an aftereffect when anti-faces are created relative to a non-average face (Anderson & Wilson, 2005). This pattern of findings is consistent with norm-based coding and the special status of the average face. The results from the current study revealed that despite their everyday difficulty in recognizing faces, the CP individuals could learn to differentiate two male faces as accurately as control individuals, and that they were as sensitive as the control group to subtle changes in identity strength as shown by their baseline performance. Most strikingly, CP individuals showed identity aftereffects comparable to those of the matched control group, which suggests that the CP individuals have some internal representation of the average face.

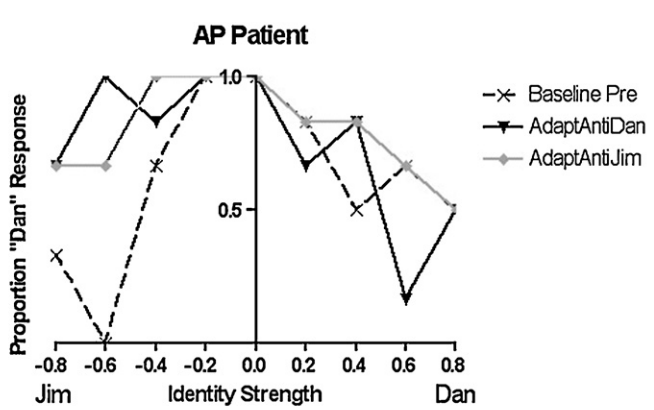

Fig. 4. Mean proportion of "Team Dan" responses as a function of identity strength for AP ($n = 1$). A sigmoidal curve could not be fit as in the data for the matched control group and the CPs.

An alternative interpretation of the findings is that the presence of facial identity aftereffects is not a sensitive test of how facial identity per se is coded. For example, there is some evidence that facial aftereffects are derived at least in part from adaptation of low-level, non-specialized neurons that are sensitive to image features that are influenced by the morphing of facial stimuli (Zhao & Chubb, 2001). A recent study has shown that simply adapting to a curved line (e.g., resembling a frown in a schematic face) that overlapped spatially with the position of the mouth of a subsequently viewed face produced an aftereffect that biased the perceived facial expression as happy (Xu, Dayan, Lipkin, & Qian, 2008). In addition, the temporal dynamics of aftereffects are similar to those of low-level visual aftereffects (e.g., Leopold, Rhodes, Muller, & Jeffery, 2005). Although there are several examples of face aftereffects surviving low-level differences between adapting and test faces (Jiang, Blanz, & O'Toole, 2006; Leopold et al., 2001; Rhodes et al., 2003; Watson & Clifford, 2003; Zhao & Chubb, 2001), it is unclear whether the identity aftereffects demonstrated by the CP individuals and the matched control participants in the current study are necessarily mediated by the same neural mechanisms. CP individuals may have differentiated Dan and Jim based on local featural cues (such as the size of the forehead or an eyebrow) (and, indeed, we know that CP individuals process visual information more locally than configurally; Avidan, Tanzer, & Behrmann, in preparation; Behrmann et al., 2005; and for AP see Barton, 2009), in which case their aftereffect should be characterized as a simple shape aftereffect rather than a facial identity aftereffect. It would be informative to extend the findings from the current study in future research by examining whether face identity aftereffects in CPs survive changes in viewpoint between adapting and test faces. Nevertheless, the AP individual did not show any systematic response to changes in identity strength, which suggests that, at the very least, intact low-level vision (as in the case of the AP individual) is not sufficient to demonstrate facial identity aftereffects (nor shape aftereffects) as shown by typical adults and CP individuals, and that this paradigm is sufficiently sensitive to reveal such abnormalities.

3. Experiment 2: Caricatures and anti-caricatures

In the previous experiment, we observed that the CP individuals showed adaptation profiles that were not differentiable from those of the control participants, whereas the AP individual's response deviated significantly from that of the control group. Although this result suggests, surprisingly, that CP individuals have some norm-based coding capacity, identity aftereffects allow us to probe only the transient bias in perceived identity of faces that are close to the average (i.e., shifts in PSE), and, as discussed above, may be indistinguishable from simple shape aftereffects. In order to assess fully the spatial layout of face-space, it is necessary to test a wide range of identities, and also to evaluate perception of faces that have been morphed away from the average so as to be more distinctive. Therefore, in Experiment 2, we used 100 facial identities and a complementary approach of testing face perception at identity strengths 50% (anti-caricatures) and 150% (caricatures).

Typically, caricatures are deformed representations of facial identities that exaggerate the distinguishing characteristics of an individual. According to the face-space framework, this process does not hinder recognition, but, rather, can enhance recognition, because it makes the face more distinctive, thereby moving the face into a low-density region of face-space. Consistent with this notion, previous research has shown that artist-drawn caricatures are recognized at least as quickly as photographs and sometimes recognized faster, even though they are, in fact, distorted representations of the true identity (Calder, Young, Benson, & Perrett, 1996; Hagen & Perkins, 1983; Rhodes et al., 1987; Stevenage, 1995; Tversky & Baratz, 1985). More recent studies have used digital

Fig. 5. The female average face, from which caricatures and anti-caricatures were computed for the caricature tasks.

morphs to produce caricatures by increasing the deviations from average, and anti-caricatures (faces that are more like the average face) by decreasing such deviations. Behavioral studies reveal that when the physical deviation from the veridical image is equated between caricatures and anti-caricatures, observers perceive the anti-caricature to be less like the veridical image than the caricature (e.g., Benson & Perrett, 1991; Lee, Byatt, & Rhodes, 2000). This pattern of results is consistent with the face-space framework because anti-caricaturing results in moving the face into a high-density region, making recognition more difficult.

In the current study, we used caricatures and anti-caricatures to probe further the nature of face-space in individuals with prosopagnosia. If faces are coded relative to the average, then caricatures should be perceived as more distinctive than anti-caricatures, and they should also be perceived as more like the original identity than anti-caricatures. We tested this hypothesis in 3 behavioral tasks using caricatures, anti-caricatures, and veridical images, by asking observers to: (1) rate the distinctiveness of faces, (2) choose the face that best resembled the original identity, and (3) decide whether two sequentially presented faces were the same or different. We examined to what extent performance on these three measures differed between individuals with prosopagnosia and controls, depending on whether a face being judged was the veridical image (100% identity strength), caricature (150% identity strength), or anti-caricature (50% identity strength). Additionally, we used 100 face stimuli to extend the findings from the previous experiment in which the morphed stimuli were created from two male identities. Taken together, the three tasks and the wide range of faces will provide a very strong probe of the abilities of the CP individuals.

3.1. Methods

3.1.1. Stimuli

For each of the three tasks described below, the same stimuli were used. Briefly, 61 male faces and 39 female faces with minimal make-up and no superfluous features were selected. The faces were drawn mainly from the Psychological Image Collection at Stirling database (PICS http://pics.psych.stir.ac.uk/) but we also included a few photographs of graduate students in the department. An average male face was created by morphing together 50 male faces and an average female face was created by morphing together 37 female faces, based on shape, texture, and color (Fig. 5). Fewer female faces were available than male faces for our experiment, but a previous study has shown that a minimum of 16 faces is sufficient to produce an identity-neutral average face, and that additional faces do not produce perceptible changes to the average face (Langlois & Roggman, 1990). We created a separate average for each gender as there is some evidence for gender-specific mental representations of average (e.g., Baudouin & Gallay, 2006; Little, De Bruine, & Jones, 2005). Caricatures and anti-caricatures were created by morphing each face to be closer to or farther away from the average by 50% using Psychomorph software (Tiddeman, Burt, & Perrett, 2001). Briefly, the interocular distance for each face was standardized, and the shape (based on 179 structural landmarks), color, and texture were morphed. A red fixation dot was applied to the center of each face using Photoshop. The procedures for each of the tasks are described below. Low-level differences across face images were minimized by blurring and equating overall brightness (see Fig. 5). Note that the three different tasks have different dependent measures (more phenomenological, subjective ratings in task 1 and more performance-based measures in tasks 2 and 3) as a means of providing a comprehensive assessment of the representations in CP.

3.1.1.1. Distinctiveness ratings. Participants viewed each face individually in the center of the screen, and rated the distinctiveness of the face on a 10-point scale, with 0 = “most typical” and 9 = “most distinctive”. Faces were caricatures, anti-caricatures, and veridical images, which remained on the screen for an unlimited duration until the participants responded with a number press on the keyboard. According to the face-space framework, caricatures should be perceived as more distinctive than veridical images, which, in turn, should be perceived as more distinctive than anti-caricatures.

3.1.1.2. Best likeness. Participants viewed three sequentially presented face images, and decided which of the first two faces was “best like” the final (target) face. The target face was always the veridical image. There were three trial types: choosing between the veridical image and its caricature, the veridical image and its anti-caricature, or between the caricature and anti-caricature of the target face. The order of pairings was counterbalanced across trials. According to the face-space framework, caricatures should be perceived as being more like the veridical image than anti-caricatures, so we would expect observers with an intact face-space to choose the caricature over the anti-caricature as best resembling the veridical image. Additionally, we would expect observers to make more errors when the choice was between a caricature and its veridical image (which is identical to the target face) than between an anti-caricature and its veridical image.

3.1.1.3. Same versus different. Participants viewed two sequentially presented face images, and decided whether the two images were the same or different. The veridical image was always shown first for 300 ms, followed by a 400 ms inter-stimulus interval showing a mask made of scrambled faces, and then a second face for 300 ms. Participants had 2000 ms to respond. On same trials (100 trials), the veridical image was shown twice. On different trials, the veridical image was followed by its caricature, its anti-caricature, or the veridical image of a different identity (100 trials per condition). To analyze the data, we calculated d' scores with hits defined as correctly responding “different” on different trials, and false alarms defined as incorrectly responding “different” on same trials. Hits were calculated separately for trials in which the “different” face was the caricature, anti-caricature, or a different identity. According to the face-space framework, caricatures should be perceived as more like the veridical image than anti-caricatures, and therefore we would expect observers with an intact face-space to have lower d' scores when the second face was a caricature than an anti-caricature (i.e. more likely to respond incorrectly that the caricature is the same as the veridical image). Performance was expected to be highest for trials in which the second face was the veridical image of a different identity, as there should be less in common between two randomly chosen faces than a face to its caricature or anti-caricature.

3.2. Results

3.2.1. Distinctiveness

Preliminary analyses comparing performance between our controls and a control group of 34 university students revealed no main

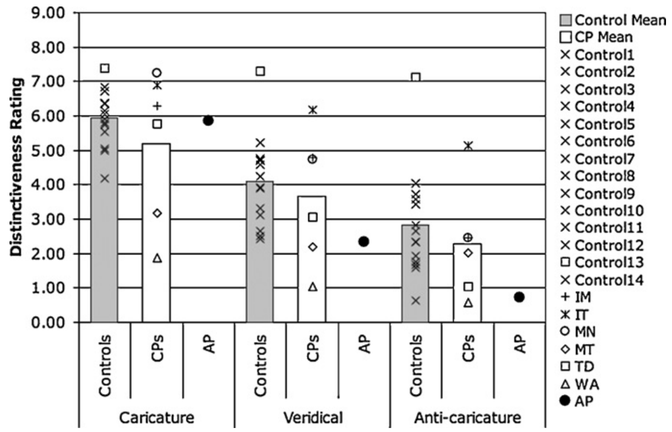

Fig. 6. Mean distinctiveness ratings for anti-caricatures, caricatures, and veridical images (original identities), for matched controls, CP group, and the AP individual.

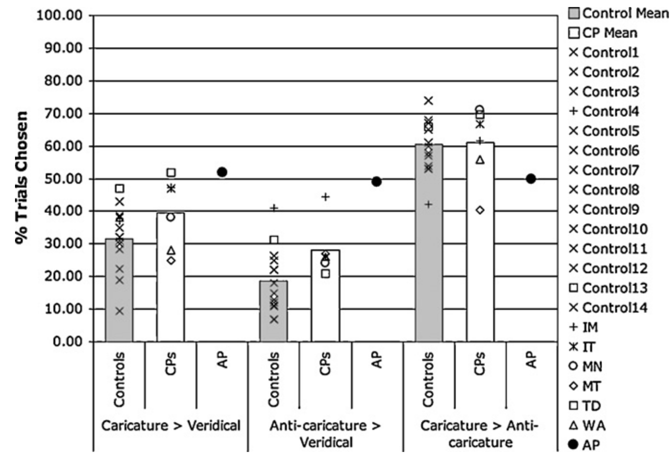

Fig. 7. Mean performance on the best likeness task of the matched controls, CP individuals, and AP individual. From the left, the figures show the % of trials in which the caricatures were chosen (erroneously) over the veridical face, the anti-caricatures were chosen (erroneously) over the veridical face, and caricatures chosen over the anti-caricature as best resembling the veridical face.

effect of *group* or interactions with *group* ($ps > 0.50$). Therefore, we judged our matched control group to be a representative sample of normal performance.

Mean distinctiveness ratings of each participant, as well as the means of the matched control and CP groups, are shown in Fig. 6. When the distinctiveness ratings of the 6 CPs and their matched controls ($n = 12$) were compared in a repeated measure ANOVA, there was a main effect of *manipulation*, $F(2, 32) = 61.55$, $p < 0.01$. Post hoc *t*-tests ($p < .05$) revealed that caricatures were rated as being more distinctive than veridical images, and veridical images were rated as being more distinctive than anti-caricatures. Importantly, there was no *group* × *manipulation* interaction, $F(2, 32) = 0.17$, $p = 0.89$, and no main effect of *group*, $F(1, 16) = 3.42$, $p = 0.46$. This pattern of findings suggests that CP individuals perceived distinctiveness in a manner similar to that of the control participants.

When the performance of individual CPs was assessed using Crawford's modified *t*-test (Crawford & Garthwaite, 2002), two CP individuals (WA and MT) rated caricatures to be significantly less distinctive than controls, and WA also rated veridical images to be less distinctive than controls. As shown in Fig. 6, WA rated all faces to be typical and did not use the full range of the scale, perhaps reflecting a failure to follow instructions. Analogously, Control Participant 13 (matched to TD, shown in open square symbol in Fig. 6) rated all faces to be highly distinctive, and her ratings for veridical images and anti-caricatures were significantly higher than the rest of the control group. Surprisingly, the AP individual's scores were all within the normal range and showed the expected pattern of caricaturing. To assess a speed-accuracy trade-off, we also compared each individual's median reaction time (RT) to the matched control group mean of the individual median RTs (mean = 2727 ms) using Crawford's modified *t*-test (Crawford & Garthwaite, 2002). All CPs (mean = 2283 ms) and the AP individual (median RT = 1919 ms) were within the normal range (1208–5599 ms).

3.2.2. Best likeness

Preliminary analyses comparing performance between our matched control group and a control group of 23 university students revealed no main effect of *group* or interactions with *group* ($ps > 0.10$). Therefore, we judged our matched control group to be a representative sample of normal performance.

Mean% of trials in which caricatures and anti-caricatures were chosen as best resembling the original identity, relative to the veridical image and relative to each other, for each individual, as well as the control and CP group means are shown in Fig. 7. The pattern of responses was similar for the controls and the CP group. The controls were more likely to choose the caricature than the anti-caricature over the (correct) veridical image, $t(13) = 3.44$, $p < 0.01$. When forced to choose between the caricature and the anti-caricature as best resembling the veridical image, controls were more likely to choose incorrectly the caricature, $t(13) = 4.71$, $p < 0.01$. Similarly, the CP individuals were more likely to choose the caricature than the anti-caricature over the veridical image, $t(5) = 2.33$, $p < 0.05$ (one-tailed), and when choosing between the two incorrect options, were more likely to choose the caricature than the anti-caricature, $t(5) = 2.33$, $p < 0.05$ (one-tailed). In contrast, the AP individual did not systematically favor the caricature over the anti-caricature, choosing the caricature roughly 50% of the time in all conditions (see Fig. 7). This pattern was unlike any CP individual.

When Crawford's modified *t*-test was applied to assess the performance of individual CPs, all individuals were within the normal range, except some individual cases: unlike controls, one CP individual (IM) and the AP individual were equally likely to choose the anti-caricature and veridical images, and one CP individual (MT) was more likely to choose the anti-caricature over the caricature (see Fig. 7). Similarly, Control Participant 13 (matched to TD) was equally likely to choose the caricature and veridical images, and Control Participant 4 (matched to IM) was more likely to choose the anti-caricature over the caricature and veridical image, unlike the rest of the control group.

3.2.3. Same versus different

Preliminary analyses comparing performance between our controls and a control group of 23 university students revealed no main effect of *group* or interactions with *group* ($ps > 0.20$). Therefore, we judged our matched control group to be a representative sample of normal performance.

D' scores of each participant, as well as the mean control and CP group performances, are shown in Fig. 8. A repeated measure ANOVA comparing the performance of CPs and the matched control group revealed a main effect of *manipulation*, $F(2, 32) = 80.43$, $p < 0.01$. Post hoc pairwise comparisons with a Bonferonni correction revealed higher d' scores for veridical different faces than anti-caricatures and caricatures ($p < .001$), and higher d' scores for anti-caricatures than caricatures ($p = .01$), a pattern consistent with the predictions of the face-space framework. Lower d' scores with caricatures suggest that caricatures were more often perceived as being the same as the veridical image than anti-caricatures, which is consistent with the results from the Best Likeness task. The per-

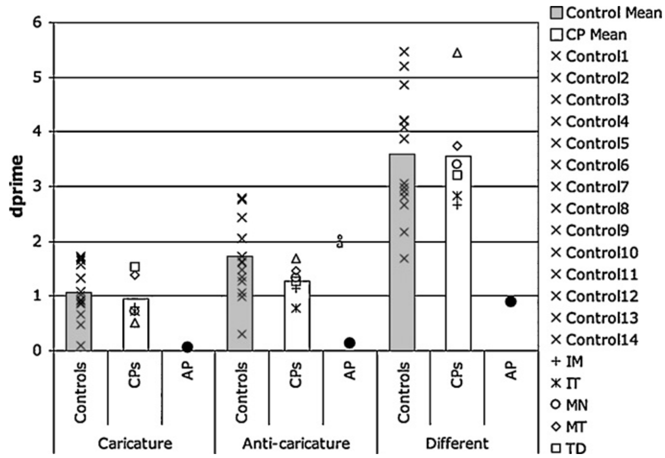

Fig. 8. Mean d' on same/different task for matched control group, CP group, and AP individual, when the veridical face was paired with its caricature, anti-caricature, or the veridical image of a different identity.

formance of the CP group did not differ from that of the control group, with no main effect of *group*, $F(1, 16) = 0.51$, $p = 0.49$, and no *manipulation* × *group* interaction, $F(2, 32) = 0.22$, $p = 0.80$.

When the performance of individual prosopagnosics was assessed, only the AP individual was significantly worse than the controls when different identities were used, and his d' scores were lower than any of the CP individuals (see Fig. 8). All CPs performed within the normal range, although IM and IT had the two lowest scores, and their scores on the Famous Faces Questionnaire (Table 1) were also the lowest of the CP group. Therefore, the poor performance of the AP individual could potentially be due to the severity of his condition rather than to a qualitative difference between AP and CP. This remains to be determined in future research.

3.3. Discussion

Collectively, notwithstanding the differences in procedures and dependent measures, the results from these three disparate tasks reveal that CP individuals perceived caricatures and anti-caricatures in a manner consistent with norm-based coding and the spatial density of a face-space layout. Like the matched controls, CP individuals rated caricatures to be more distinctive than anti-caricatures, and perceived the caricatures to be more like the veridical face than anti-caricatures. These findings, consistent with the results from Experiment 1, again suggest that CP individuals have some representation of faces that resemble a face-space structure. Conversely, the AP individual's performance when making same/different and similarity judgments did not reveal typical caricature effects. Surprisingly, the AP individual judged distinctiveness of the caricatures and anti-caricatures in a manner predicted by the face-space framework, and there did not appear to be a speed-accuracy trade-off. The source of his perception of distinctiveness despite his inability to perceive caricatures to be more like the veridical face than anti-caricatures are discussed in Section 5.

The results also showed that there was individual variability in perceiving caricatures and anti-caricatures. Although no single participant's performance (in either the control or CP groups) deviated significantly from the norm on all three tasks, in both the distinctiveness task and the best likeness task, there were some individuals who performed differently from (the rest of) the control group, which shows that there is some variability even in the normal population on how caricatures and anti-caricatures are perceived. Therefore, no one task from the present study can be used as a diagnostic test for prosopagnosia, but the consistency across tasks is highly informative.

Fig. 9. Examples of a typical face (left) and a distinctive face (right) used for multi-dimensional scaling analysis.

4. Experiment 3: Similarity judgments and multi-dimensional scaling

Studies examining face identity aftereffects and caricature effects provide insight into norm-based coding and the spatial density of face-space, but cannot elucidate whether prosopagnosics and controls utilize different dimensions of face-space. In his original proposal, Valentine (1991) did not specify what the dimensions of face-space represent, only that they represent facial characteristics that are important for face discrimination and recognition. One approach to exploring the dimensions of face-space is to use multi-dimensional scaling (MDS), a statistical procedure that represents perceived similarity among pairs of items as distances between points in a multi-dimensional space, often revealing regularities that remain hidden if the raw similarity judgments are examined directly (Borg & Groenen, 2005). Therefore, we asked individuals with prosopagnosia and control participants to rate the similarity of pairs of faces, and conducted MDS on those ratings (Nishimura et al., 2009). The previous two experiments used faces that were morphed relative to a digitized average face, allowing an examination of perceived identity as faces are moved closer to or farther away from the average. In contrast, here, we examined how prosopagnosics perceive the identity of faces without morphing. The faces were manipulated, however, to have the same hairstyle (see Fig. 9) because individuals with prosopagnosia can sometimes successfully discriminate faces based solely on external hair cues (e.g., Duchaine & Nakayama, 2006; Schmalzl, Palermo, Green, Brunsdon, & Coltheart, 2008; Stephan & Caine, 2009).

4.1. Methods

4.1.1. Stimuli and procedure

Participants viewed pairs of faces presented simultaneously, and rated their similarity on a 7-point scale, ranging from 1 = "very similar" to 7 = "very different". All 25 faces had the same hair morphed onto their heads (Fig. 9), so that similarity judgments must necessarily be based on the internal characteristics of the faces. Participants saw every possible pairing of 25 women's faces, for a total of 300 trials. The faces had been ranked on their distinctiveness previously by a group of university students (see Nishimura et al., 2009). Faces remained on the screen for an unlimited duration until the participant pressed a number on the keyboard. The procedure was self-paced and participants took breaks as needed. The raw ratings were then subjected to multi-dimensional scaling analysis.

4.2. Results

Prior to the MDS analysis, we compared the mean similarity ratings for each pair of faces from the matched control group to the CP group and AP individual. There was a significant correlation between the matched control group and the CP group, $r(298) = 0.731$, $p < 0.001$, which was similar in magnitude to the split-half correlation of the matched control group, $r(298) = 0.734$, $p < 0.001$. The correlation between the matched control group and the AP individual was not significant, $r(298) = 0.058$, $p = 0.32$. Although statistically significant, the correlation between the CP group and the AP individual was much lower than that between the CP and matched control group, $r(298) = 0.130$, $p < 0.05$.

A similarity matrix was constructed for each individual from his/her raw similarity ratings for every possible face pair, and these individual matrices were subjected to multi-dimensional scaling analysis using the ALSCAL function in SPSS 16.0. The goodness-of-fit for the 2–6-dimensional scaling solutions was measured by Kruskal's Stress 1 formula (Kruskal & Wish, 1978) and is shown in Fig. 10. Lower values indicate a better fit of the MDS solutions to the raw similarity ratings, and to help interpret the goodness-of-fit, Stress values collected previously from a group of 24 university-aged students are also shown for comparison (Nishimura et al., 2009). The fit of all solutions was comparable across the two control groups and the CP group. Although there are no standard guidelines for assessing Kruskal's Stress values (Giguere, 2006), the fit of the 5-dimensional solution (Stress = 0.21) and the 6-dimensional solution (Stress = 0.18) are comparable to those previously reported to be good fits (e.g., Stress = 0.14 in Johnston, Milne, & Williams, 1997; 0.19 in Lee et al., 2000; 0.26 in Yotsumoto, Kahana, Wilson, & Sekuler, 2007), and consistent with previous findings showing 5 dimensions to be optimal to account for adults' similarity judgments (Nishimura et al., 2009). The fit of the solutions for the AP individual was better than these values, but this was expected because data from a single observer can be better fit with fewer dimensions.

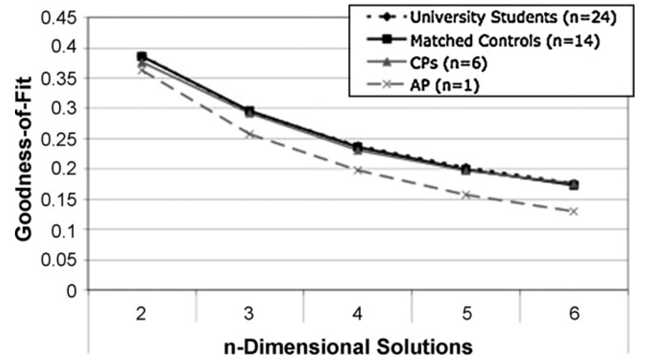

Fig. 10. Goodness-of-fit (assessed by Kruskal's Stress 1 formula) of the 2–6-dimensional scaling solutions. Lower values indicate better fit.

Because it is difficult to compare 5D solutions visually, we show the 2D solutions in Fig. 11. Visual inspection suggests that faces were positioned similarly in the solutions from the control and CP

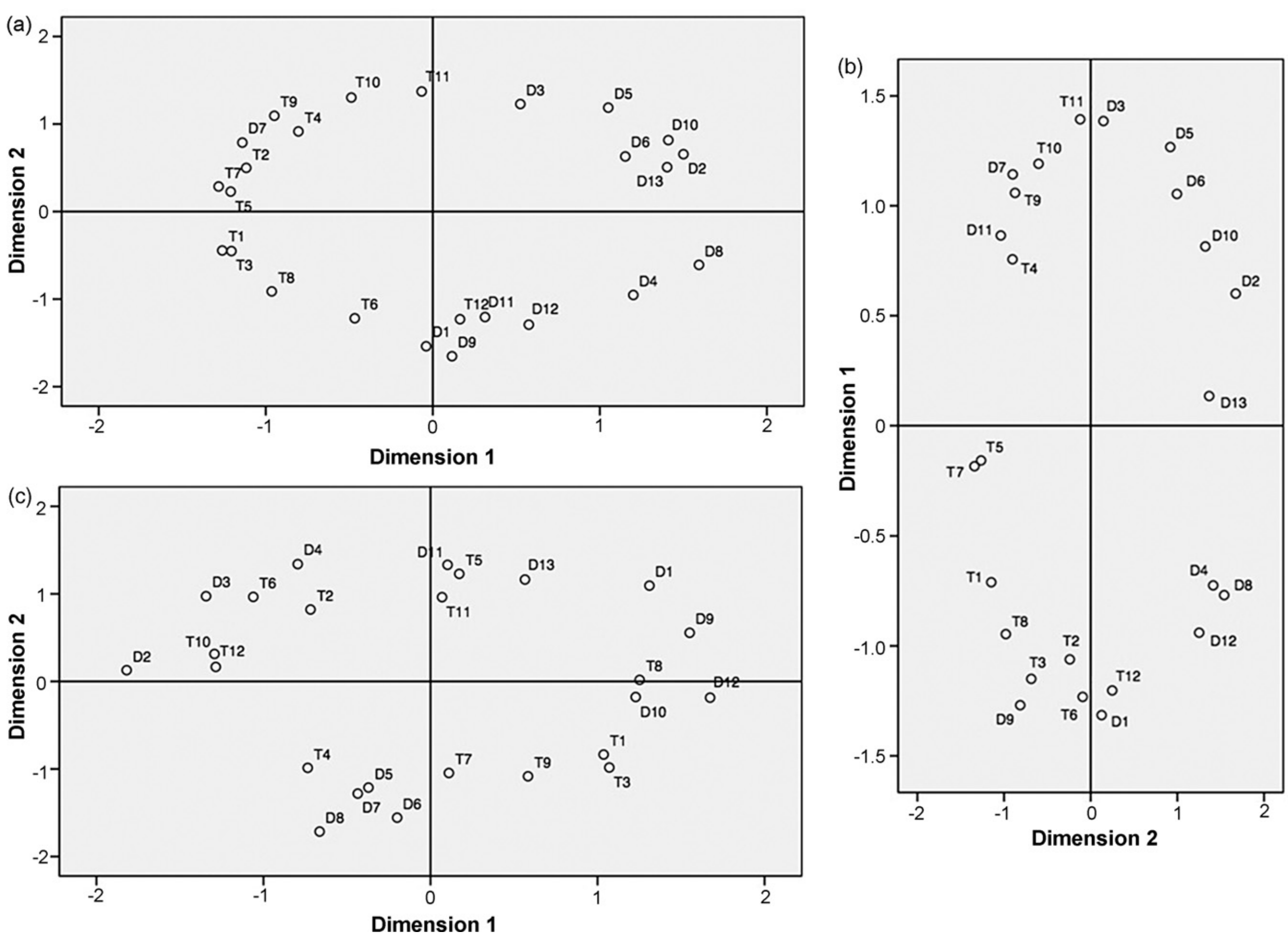

Fig. 11. Two-dimensional MDS solutions for (a) matched control group, (b) CP group, and (c) AP individual. Each circle represents a face stimulus, with 13 distinctive faces (D1–D13; D1 = most distinctive) and 12 typical faces (T1–T12; T1 = most typical). Dimension 1 for the matched control group and Dimension 2 of the CP group appears to code for typicality/distinctiveness, whereas no such structure is observed in the solution of the AP individual.

Table 2
t-Tests comparing the distance to the origin of distinctive versus typical faces for 2–6-dimensional MDS solutions of the matched control group, CP group, and CP patient.

	2D	3D	4D	5D	6D
Matched control group	$t(23) = 4.03$ $p < .01$	$t(23) = 6.51$ $p < .001$	$t(23) = 6.05$ $p < .001$	$t(23) = 3.49$ $p < .01$	$t(23) = 1.63$ $p = .12$
CPs	$t(23) = 4.53$ $p < .001$	$t(23) = 5.58$ $p < .001$	$t(23) = 5.59$ $p < .001$	$t(23) = 6.51$ $p < .001$	$t(23) = 5.18$ $p < .001$
AP	$t(23) = 3.98$ $p < .01$	$t(23) = 2.51$ $p < .05$	$t(23) = 1.53$ $p = .14$	$t(23) = 1.50$ $p = .15$	$t(23) = 1.38$ $p = .18$

groups, but not in the solution of the AP individual.[2] Furthermore, Dimension 1 of the control group and Dimension 2 of the CP group appear to code for typicality/distinctiveness (because distinctive faces appear on one side of the solution and typical faces on the other), whereas no such structure is observed in the solution of the AP individual. Although visual inspection is easiest for the 2D solutions, a previous study using the same stimuli had established the 5D solution to be optimal for representing adults' similarity ratings (Nishimura et al., 2009). Because it is impossible to represent a 5D solution on a 2D surface for visual inspection, we conducted hierarchical cluster analysis using the pairwise distance among faces in the 5D solution to assess the similarity of the relative positions of faces across the solutions from the three groups (see Fig. 12). By taking intermediate-size clusters of 3–6 faces (i.e. the smallest clustering that avoids clusters with only one face), we can see that 5 out of 6 clusters that appeared in the solution of the control group were similarly present in the solution of the CP group (18/25 faces overlap). Conversely, when the clusters of the control group were compared to the clusters of the AP individual, only three pairs of faces clustered together similarly, and 3/6 clusters showed no overlap (see Fig. 12). These findings suggest that the coarse layout of the MDS solutions was similar between the matched control group and the CP group, but not between the matched control group and the AP individual.

To examine the role of distinctiveness on the similarity judgments, we calculated the distance of each face from the origin in each MDS solution (2–6 dimensions), separately for the matched control group, CP group, and the AP individual. As predicted by the face-space framework, *t*-tests revealed that the distance to the origin for typical faces was smaller than the distance for distinctive faces, for all solutions for the matched control group except the 6D solution (confirming that the 6D solution is not optimal for the control group), and all solutions for the CP group (Table 2). However, only the 2D and 3D solutions of the AP individual showed the expected pattern of distinctiveness, which suggests that even when the AP individual is making distinctiveness judgments in a manner similar to typical adults (results from Experiment 2), he is utilizing fewer dimensions than in visually normal adults and the CP group.

4.3. Discussion

Collectively, the results suggest that the CP individuals perceive similarity of faces in a pattern similar to that of the matched control group. Conversely, the AP individual's ratings were not significantly correlated with those of the matched control group, and his MDS solutions did not resemble those of the control group, as revealed by the 2D solutions and the cluster analysis of the 5D solutions. A previous study using the same stimuli revealed that the dimensions of the MDS solutions likely represent adults' use of an amalgam of facial characteristics that cannot be easily verbalized, with emphasis on the eyes and mouth (Nishimura et al., 2009). Although the dimensions are not transparently and intuitively identifiable (i.e., it is not that the participants are rating the interocular distance or roundness of the eyes, for example; see also Catz, Kampf, Nachson, & Babkoff, 2009), what is critical here is that the CP individuals' perceptual judgments were not differentiable from those of the matched control group, suggesting that CP individuals were utilizing cues that were similar to those used by the control participants to make their similarity judgments. The findings are consistent with the interpretation that CP individuals have a mental representation of facial identity that, at the very least, coarsely resembles the face-space of typical adults.

5. General discussion

The goal of this study was to explore the nature of the underlying representations of faces in individuals with congenital prosopagnosia. The results reveal that, interestingly and indeed surprisingly, CP individuals have a mental representation of faces that is largely consistent with typical adult face-space. Conversely, our single AP case revealed a pattern that differed from both the CP and matched control groups, which, importantly, suggests that our measures were sufficiently sensitive to reveal abnormalities in face perception should they exist. Across a range of five behavioral tasks designed to assess identity aftereffects, caricature effects (three subtasks), and similarity judgments of facial identity, the performance of CP individuals was statistically not differentiable from that of a group of age- and gender-matched controls. Although only six CPs were tested in the current study, the results from the ANOVAs are confirmed and supported by statistical analyses of single subject data using Crawford's modified *t*-test (Crawford & Garthwaite, 2002), which showed that individual CP performance typically fell within the normal range. CP individuals learned to recognize successfully two male faces and their weaker identity morphs, showed similar identity aftereffects after adaptation, rated caricatures to be more distinctive and more like the original identity than anti-caricatures, and judged the similarity of non-morphed faces in a pattern similar to control participants. The findings from the different tasks converge robustly to support the conclusion that the CP individuals have, at the very least, a coarse mental representation of faces with a similar structure to the mental representation of facial identity in typical adults, at the center of which is the average of previously encountered faces. These findings are consistent with recent studies, which show that CP individuals demonstrate some implicit memory of famous faces (e.g., Avidan et al., 2008; Bate, Haslam, Tree, & Hodgson, 2008; Striemer, Gingerich, Striemer, & Dixon, 2009), which, too, indicate that they have some mental representation of individual facial identities, even if these cannot be accessed explicitly. The results are consistent with the interpretation that CP individuals have a coarse "face-space" that suffices under some conditions (e.g., perceiving typicality/distinctiveness and similarity of faces) but is insufficient for explicit individual recognition.

In contrast with the CP findings, the AP individual showed a different pattern: he was unable to recognize consistently the newly

[2] Because only relative positions, and not absolute positions, of items in MDS solutions are meaningful, the solution of the CP group has been rotated for ease of comparison.

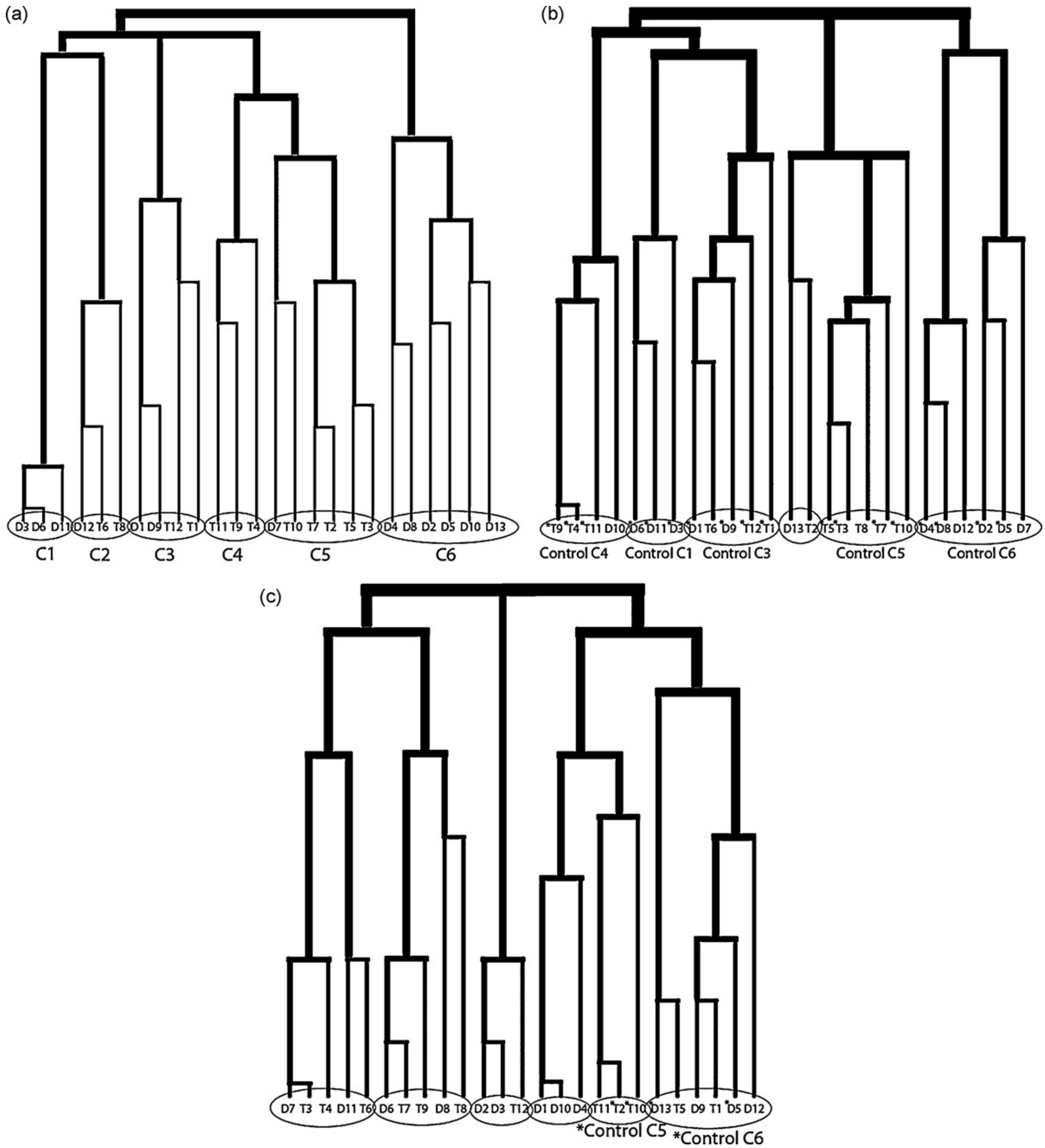

Fig. 12. Local clustering of faces in the 5-dimensional MDS solutions for (a) matched control group, (b) CP group, and (c) AP individual. Charts should be read from bottom to top, with each horizontal bar indicating a clustering based on perceived similarity. To allow comparison across groups, faces in the solution for the control group were clustered into groups of 3–6 faces. We then visually inspected whether similar groups formed in the solution for the CP group and AP individual. *Faces that fell into the same cluster as in the solution for the control group.

learned identities even though he was able to learn them initially, and he was unable to perceive the difference among caricatures, anti-caricatures, and veridical images. The local clustering of the faces in the MDS solution also diverged significantly from the MDS solutions of the CP and matched control groups. Collectively, the findings suggest that this individual with acquired prosopagnosia, and perhaps others too, may be unable to recognize facial identity because their internal face-space has been adversely affected by the insult to the brain. The findings from the AP individual also suggest that the performance of the CP group cannot be attributed solely to their intact low-level visual capacities nor to the poor resolution of the particular experiments as these tasks are clearly sensitive enough to uncover abnormalities where they exist.

Because we only had one AP individual in our sample, it is difficult to assess whether his impairments revealed in the present study are due to the severity of his prosopagnosia. As summarized in Table 1, it is the case that the AP individual's recognition of famous faces was worse than any other CP individual (although his RT is not the slowest, which suggests some speed-accuracy trade-off, as discussed in Behrmann & Avidan, 2005). CP individuals IM and IT had the worst recognition accuracy of the CP group, and these two individuals had the smallest identity aftereffect in the expected direction (Fig. 3), and the worst d' scores when judging veridically different faces, which suggest some predictability of our tasks based on the severity of the face recognition deficit. However, there was no clear pattern of atypicality in perceiving caricatures and anti-caricatures by individuals IM and IT, which indicates that the severity of the condition does not predict all types of perceptual judgments. Despite the possibility that the AP individual's performance on the present tasks represents the severity of his condition, a dissociation between these two types of prospagnosia has been suggested by a previous finding in which CP, but not AP individuals (matched in severity to some of the CP participants), were able to make fine discriminations between faces with subtle emotional expressions (e.g., a face with 60% happiness and 40% disgust is still identified as 'happy'; Humphreys, Avidan, & Behrmann, 2007).

5.1. The 'face-space' profile of CP and its possible neural instantiation

One immediate question is how it is possible that CP individuals possess an apparently normal face-space along with their face recognition impairment. The results suggest that a mental representation of "average" can exist independently of accurate and stable representations of the individual faces that went into creating that average, because CP individuals fail to recognize even highly familiar faces despite normal performance in the current study. How is such a mental representation of the average derived or computed?

CP individuals can classify visual stimuli as being a face or not a face (Behrmann, Avidan, Gao, & Black, 2007; Garrido, Duchaine, & Nakayama, 2008; Lee, Duchaine, Wilson, & Nakayama, 2009), perhaps, in part, because they can perceive the local features (Behrmann et al., 2005; Le Grand et al., 2006; Nunn, Postma, & Pearson, 2001; but see also Yovel & Duchaine, 2006 for inability to discriminate small changes to feature shapes). Many CP individuals have also been shown to demonstrate an inversion superiority effect: better discrimination of inverted than upright faces, which can be explained by an undue reliance on local features to judge facial identity (Behrmann et al., 2005). Therefore, one interpretation of the present findings is that the mental representation of faces in CP individuals relies on local facial characteristics, and such a representation has a similar general structure to typical adults' face-space. When salient featural cues are available to discriminate faces, typical adults also rely on local characteristics such as face width, facial hair, and forehead size (Busey, 1998; Johnston et al., 1997). However, when similarity and identity judgments are required of a homogenous set of face stimuli, typical adults appear to utilize an amalgam of facial characteristics, including the spatial relations among facial features (Mondloch, Le Grand, & Maurer, 2002; Nishimura et al., 2009). The claim then is that the intact perception of local features suffices to generate a coarse representation of facial identity that is consistent with the face-space framework, but it is unclear to what extent the fine-grained characteristics of the dimensions underlying this representation differ between CP individuals and typical adults.

This hypothesis is then consistent with the proposal that the difficulty experienced by CP individuals in identifying individual faces appears to stem from an inability to 'glue' such local features together to create a whole percept representing facial identity (Avidan, Thomas, & Behrmann, 2008; Barton, Press, Keenan, & O'Connor, 2002; Bentin, DeGutis, D'Esposito, & Robertson, 2007; Le Grand et al., 2006; but see Duchaine, 2000 for a report of a CP who was sensitive to the configurations of objects and scenes), a process that typical adults can do automatically and effortlessly (e.g., Mondloch et al., 2002; Tanaka & Farah, 1993; Young, Helawell, and Hay, 1987). Perhaps CP individuals have developed a compensatory mechanism that over-relies on featural cues in an effort to distinguish individual faces. Support for this claim comes from a study that shows that 10 individuals with CP do not make false alarms on a composite face task (Avidan et al., in preparation). Typically, in such a task, controls make errors in judging the tops of two faces as different when they are really the same and, hence, appear to be influenced by the difference in the two lower parts of the faces when the tops and bottoms are aligned. In contrast, CP individuals appear impervious to the status of the task-irrelevant lower part of the faces even when the upper and lower parts are aligned, suggesting that these individuals rely on more local aspects of the face and do not automatically process the entire configuration of the face. Additionally, training specifically on discriminating changes to the interrelations among facial features improved a CP individual's ability to recognize faces in daily life and increased the connectivity between neural structures supporting face recognition (De Gutis, Bentin, Robertson, & D'Esposito, 2007).

The results of the current study suggest, then, that the ability to process local features may suffice to set up a coarse face-space representation. For example, because the faces were morphed in such a way that the size of all facial characteristics were changed simultaneously, it is conceivable that an observer who perceives the face as a whole and an observer who attends to a specific local feature may show similar aftereffects and caricature effects. In terms of a face-space framework, CP individuals and controls may show similar performance because the feature representing Dimension 1 in the CP face-space may also be a part of the amalgam of features represented in Dimension 1 of typical adult face-space. In addition, there must be some underlying structure to the mental representation of local features in the CP individuals that is consistent with norm-based coding, because the AP individual, who can process local features if given sufficient time (Behrmann & Kimchi, 2003), performed differently from the controls and CPs in the present study.

The face-space framework is a theory of the cognitive representation of facial identities, and, therefore, makes no specific predictions about the neural locus of face-space. The findings from the current study, however, place some constraints on our understanding of the neural basis of this cognitive map. One implication of the current findings is that face-space, or at least the representation of "average", is likely coded in neural areas that have similar response dynamics in CP individuals and typical adults. One possible candidate for this is the fusiform face area or the FFA (Kanwisher, McDermott, & Chun, 1997), because like typical adults, many (although not all) CP individuals demonstrate normal face-selective activity and BOLD reduction in response to adaptation in the FFA (Avidan & Behrmann, 2008; Avidan, Hasson, Malach, & Behrmann, 2005). Furthermore, FFA appears to be involved in the processing of local facial features, as it responds to both featural and configural manipulations to facial stimuli (Liu, Harris, & Kanwisher, 2010; Maurer et al., 2007), and it responds to facial fragments that are important for face detection (Nestor, Vettel, & Tarr, 2008). These findings suggest that the FFA activation demonstrated by CP individuals could arise from the structural encoding of local facial features. Furthermore, facial identity aftereffects appear to be viewpoint-specific (Jeffery, Rhodes, & Busey, 2006; Morikawa, 2005), , which suggests that aftereffects occur before the stage in which face representations acquire viewpoint-invariance. fMR-adaptation in the FFA is observed with repeated presentations of the same face in different sizes, but not with different viewpoints (Anderson & Wilson, 2005; Andrews & Ewbank, 2004), which suggests, further, that the FFA may be the neural correlate of face distortion aftereffects. Indeed a recent study has shown that when the perceptual face adaptation aftereffect was larger, there was greater fMR-adaptation in the FFA (Cziraki, Greenlee, & Kovacs, 2010).

However, it is also becoming increasingly recognized that the FFA alone does not suffice for intact face recognition. For example, there are some AP individuals who demonstrated normal FFA activation but a lack of OFA activation (Steeves et al., 2006, 2009), a result suggesting that the FFA is not sufficient for normal face processing. Furthermore, several recent studies suggest that face processing involves a distributed network of cortical areas (e.g., Gobbini & Haxby, 2007; Haxby et al., 2001; Haxby, Hoffman, Gobbini, 2000; Hoffman & Haxby, 2000; Ishai, 2008; Ishai, Ungerleider, Martin, Schouten, & Haxby, 1999; Puce, Allison, Bentin, Gore, & McCarthy, 1998; Rossion et al., 2003), and, therefore, future studies should examine to what extent norm-based coding and recognition of individual facial identities are supported by different neural mechanisms. Indeed, one related recent finding is that the white matter tracts that connect the posterior regions of this distributed network, including the FFA, are compromised in individuals with CP (Thomas et al., 2009), perhaps resulting in decreased volume in the anterior temporal lobe (Behrmann et al., 2007; Garrido et al., 2009), and it may be this apparent disconnection from the core posterior areas (which may subserve face-space) and the more anterior areas that account for the behavioral profile of CP.

5.2. The 'face-space' profile of AP and its possible neural instantiation

In contrast with some preservation of face-space in CP, the AP individual evinces little evidence of sensitivity to the internal structure of this underlying mental map. Presumably, this individual had acquired a normal face-space premorbidly. Note that this individual has a lesion that implicates the right FFA but that more posterior and more anterior regions are preserved. Given our claim that FFA plays a critical role in encoding the geometry of the incoming stimulus and perhaps computing parameters of face-space, the lesion in this individual may have affected the structure of the internal face-space. However, one aspect of face processing appears to be intact, because his perception of distinctiveness was not different from the controls. One possible explanation for his performance is that he has a stable representation of prototypical facial features, which allows him to make typical judgments of "normality", but that he is unable to encode and/or retrieve *individual* features, which would be necessary to show typical aftereffects or "best likeness" judgments. Such a deficit in processing local features likely extends beyond face stimuli, because this AP individual was much slower than controls even when making judgments just about the local letters in hierarchical letter stimuli (Behrmann & Kimchi, 2003). Of course it will be essential to replicate the findings with other AP individuals to verify the generalizability of the result and, moreover, depending on their lesion site, to begin to make more precise inferences about the brain-behavior relationships within the face-space conceptual framework. Our inclusion of this participant in our sample served mainly to verify that our measures were sufficiently sensitive to reveal abnormalities where they exist, and his data are insufficient for making general claims about differences between the behavioral profiles of CP and AP. While the AP individual's data are intriguing in and of themselves, further exploration is clearly warranted before definitive conclusions are possible.

6. Conclusion

In sum, the findings suggest that CP individuals demonstrate face processing abilities that are consistent with the face-space framework, whereas the AP individual does not. This result indicates that CP individuals have a coarse, perhaps feature-based face-space that is subserved in neural areas, such as the FFA, that are intact, but that individual recognition of faces involves more anterior areas beyond the FFA.

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