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RESEARCH ARTICLE

A detailed investigation of facial expression processing in congenital prosopagnosia as compared to acquired prosopagnosia

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Abstract Whether the ability to recognize facial expression can be preserved in the absence of the recognition of facial identity remains controversial. The current study reports the results of a detailed investigation of facial expression recognition in three congenital prosopagnosic (CP) participants, in comparison with two patients with acquired prosopagnosia (AP) and a large group of 30 neurologically normal participants, including individually age- and gender-matched controls. Participants completed a fine-grained expression recognition paradigm requiring a six-alternative forced-choice response to continua of morphs of six different basic facial expressions (e.g. happiness and surprise). Accuracy, sensitivity and reaction times were measured. The performance of all three CP individuals was indistinguishable from that of controls, even for the most subtle expressions. In contrast, both individuals with AP displayed pronounced difficulties with the majority of expressions. The results from the CP participants attest to the dissociability of the processing of facial identity and of facial expression. Whether this remarkably good expression recognition is achieved through normal, or compensatory, mechanisms remains to be determined. Either way, this normal level of performance does not extend to include facial identity.

Keywords Prosopagnosia · Facial expressions · Emotion · Congenital versus acquired · Cognitive neuropsychology · Face processing

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Introduction

Prosopagnosia is the inability to recognize faces. Acquired prosopagnosia (AP), following stroke or head injury, has been documented since the early report of Bodamer (1947) and there are now many detailed investigations of individuals with AP (for review, see Behrmann and Moscovitch 2001; Farah 2004). AP involves, by definition, deficits in facial identity processing, but is also often associated with difficulties in aspects of face processing other than facial identity, particularly facial expressions (e.g. Bowers et al. 1985; de Gelder et al. 2000; De Renzi and Di Pellegrino 1998; Humphreys et al. 1993). In fact, Calder and Young (2005), in a recent review, have challenged the claim that some prosopagnosic individuals show preserved facial expression recognition and suggest that the dissociability of identity and expression processing is less well supported by patient-based research than has been widely assumed (p 643). They state that the assertion that these individuals can process facial expressions normally is largely based on anecdote and that, on formal testing, impairments on expression recognition are usually uncovered in these individuals. On their account, only two reports (Bruyer et al. 1983; Tranel et al. 1988) offer evidence of prosopagnosia

with preserved facial expression recognition but even then, there still remain open questions about these two studies. Whether the recognition of identity can indeed be dissociated from that of facial expression processing is of much import in that many major theoretical models of face processing (for example, Bruce and Young 1986; Haxby et al. 2000) postulate separate functional (and neural) routes for these two processes.

To address the possible dissociability of identity and expression processing, in this paper, we examine the performance of an unusual group of individuals, who have been the subject of an increasing number of recent investigations, and who, like the AP individuals, have a marked deficit in facial identity processing. In contrast with AP, however, these individuals, with congenital prosopagnosia[1] (CP) exhibit severe life-long difficulties with face recognition in the absence of any known neurological alteration (see Behrmann and Avidan 2005; Duchaine and Nakayama 2006a; Kress and Daum 2003a, for reviews). The key question is whether CP, like AP, is associated with expression recognition deficits. Naturally, most investigations of CP have concentrated on facial identity processing. To the extent that facial expression processing has been addressed, the picture is mixed, with some reports that facial expression processing is intact in CP (Bentin et al. 1999; Duchaine et al. 2003a; Jones and Tranel 2001; Nunn et al. 2001) and others finding impairments (e.g. Ariel and Sadeh 1996; Campbell 1992; Duchaine et al. 2003b, 2004; Kracke 1994).

Although, at first blush, it appears that CP may be heterogeneous with respect to facial expression impairments, a close reading of the literature suggests that this may not be the case. Firstly, several of the cases in which expression recognition difficulties have been found are reported to have comorbid autism spectrum disorders (Duchaine et al. 2003b; Kracke 1994). Since autism spectrum disorders are themselves associated with facial expression deficits (see e.g. Humphreys et al. 2006; Tantam et al. 1993), it is not clear that we can reach any conclusions about CP per se from these examples. It is also difficult to reach any conclusions from the patient of Campbell (1992; see also de Haan and Campbell 1991; McConachie 1976), who appears to have neurological abnormalities (atypical spiking in her EEG, p 217) and more widespread, non-visual neurological problems, such as poor fine motor control and untidy writing. Indeed, the only 'pure' case of CP to date in whom facial expression deficits have been reported appears to be that of Ariel and Sadeh (1996): L.G., an 8-year-old visual agnosic and prosopagnosic, was only 20% correct when asked to recognize pictures of happiness, sadness, anger and neutrality. L.G. was socially well adjusted but did have an unusual, repetitive 'blinking habit' (p 233). Although the authors believe it was simply an attempt to avoid visual overstimulation, it may also represent a tic or obsessive behavior, which could be suggestive of a more widespread developmental disorder.

Given the findings from the cases above, the evidence favoring impairment in facial expression processing in CP that has a visuoperceptual basis remains equivocal. On the other hand, detailed reports of intact expression processing in CP are few in number. In one (Bentin et al. 1999), facial expression abilities do not appear to have been formally tested, and Jones and Tranel (2001) used a very simple two-alternative choice task. However, detailed case studies of adults with CP (Duchaine et al. 2003a; Kress and Daum 2003b; Nunn et al. 2001), find no evidence of facial expression deficits. Neither of these individuals had any known non-visual functional deficits or neurological abnormalities. Nunn et al. (2001) reported that their patient, EP, performed normally on a six-alternative forced-choice response task with the six basic expressions from the Ekman and Friesen (1976) set, and in an extensive investigation of facial expression recognition and perception, employing morphed expressions of different intensities, Duchaine et al. (2003a) failed to find any evidence of an expression impairment in an adult with CP.

In summary, while findings of expression impairment are mixed, in all the CP cases, to our knowledge, where expression deficits have been reported, there is some suspicion of coexisting more widespread neurological or psychopathological difficulties; these latter difficulties might, in themselves, account for the facial expression recognition deficits. In contrast, there have been a few detailed case studies that have found no evidence of expression deficits in CP, but these are limited in that they discuss only single patients and their methods of assessment are quite varied. The purpose of the present set of studies, then, is to investigate, in some detail, the facial expression recognition abilities in three CP individuals, all of whom have been carefully selected to avoid any coexisting neurological, psychiatric or social difficulties.

Here, we compare the facial expression recognition of these three CP individuals with that of a large group of 30 neurologically normal controls, including individually age- and gender-matched controls. We also con-

[1] We distinguish this from the more general term 'developmental prosopagnosia', which encompasses both the congenital cases and those caused by brain injury or any known neuropathology during development.

trast their performance with that of two acquired prosopagnosics (AP). Both the CP and AP individuals are impaired to approximately the same extent at identity processing and our question is whether they are similarly impaired at other aspects of face processing too. We first document the nature and extent of the facial identity processing deficit in all the prosopagnosic participants. We then turn to the critical experiments and present a fine-grained test of facial expression processing, using morphed facial expressions of the six basic expressions and taking measures of both accuracy and reaction times. This detailed experiment allows us to explore facial expression recognition thoroughly in our group of individuals with CP, and to compare it, not only with normal performance, but also with performance by individuals who are impaired at facial identity processing.

Method

Participants

All participants voluntarily consented to take part in the study, which was approved by Carnegie Mellon and the University of Pittsburgh Institutional Review Boards, and therefore conformed to the ethical standards laid down in the 1964 Declaration of Helsinki.

Participants with CP

The three participants with CP were KM (CP1), a 60-year-old female, MT (CP2), a 42-year-old male and TM, a 28-year-old male (CP3), all of whom have participated in our previous experiments (see Avidan et al. 2005; Behrmann et al. 2005a). All are right-handed with no neurological or neuropsychological deficit aside from the impairment in face processing. In particular, none shows any evidence of any social deficit; potential participants suspected of falling along the autism spectrum were specifically excluded. All have visual acuity of, or corrected to, 20/20, and their basic visual processing abilities (spatial frequency thresholds and Gabor contour detection) are unimpaired (Behrmann et al. 2005a). None shows any obvious cortical changes on structural MRI although there may be more subtle structural and volumetric changes in temporal cortex (Behrmann et al., submitted; see also Bentin et al. 1999) and all show normal face-related activation in face selective brain regions across a number of different functional MRI experiments (Avidan et al. 2005; see Hasson et al. 2003 for a similar report, and also von Kriegstein et al. 2006).

Participants with AP

The two patients with AP were RN (AP1) and SM (AP2). RN, described previously (Behrmann and Kimchi 2003; Marotta et al. 2002), is a 49-year-old right-handed male who suffered an anoxic episode following myocardial infarction in 1998. A recent MR scan (Fig. 1a) revealed several gross abnormalities (enlarged ventricles, widespread atrophy, most marked in bilateral parieto-temporal regions) and density inhomogeneities in occipitotemporal areas. His corrected visual acuity is 20/20 and he has normal color vision. SM, who has also participated in previous studies (Behrmann and Kimchi 2003; Behrmann et al. 2005b; Gauthier et al. 1999; Marotta et al. 2001) is a right-handed male who was 30 years old at the time of testing. SM sustained a closed head injury and loss of consciousness in a road traffic accident in 1992. He has a contusion in the right anterior and posterior temporal regions (see Fig. 1b for a recent MR scan) and a deep shearing injury in the corpus callosum and left basal ganglia was reported on a previous scan. His vision is corrected to 20/20, and his color vision is normal. Experimental testing of the AP participants took place in late 2004 (6 years post-onset for RN and 12 years post-onset for SM) and the structural MR scans presented here were acquired shortly afterwards in early-mid 2005.

Both patients had normal spatial frequency thresholds (Behrmann and Kimchi 2003) and both performed normally on the subtests of the Birmingham Object Recognition Battery (BORB; Riddoch and Humphreys 1993) tapping early visual processes, including judging line length, orientation, size, and gap position. Both also performed in the normal range on more complex visual tasks (matching objects on the basis of minimal features or when one object was foreshortened). Both could copy drawings reasonably well, although slowly and in a piecemeal fashion (Behrmann and Kimchi 2003). They were both impaired on the BORB subtest that evaluates discrimination of overlapping shapes and on the object decision subtests.

Neurologically normal control participants

Control participants were community volunteers and undergraduate students with no history of neurological or psychiatric illness. For each experiment, two age- and gender-matched controls were used for each AP and CP prosopagnosic individual, and data from an additional 20 neurologically normal individuals were also added to form a large comparison sample ($N = 30$). All participants gave written informed consent and all

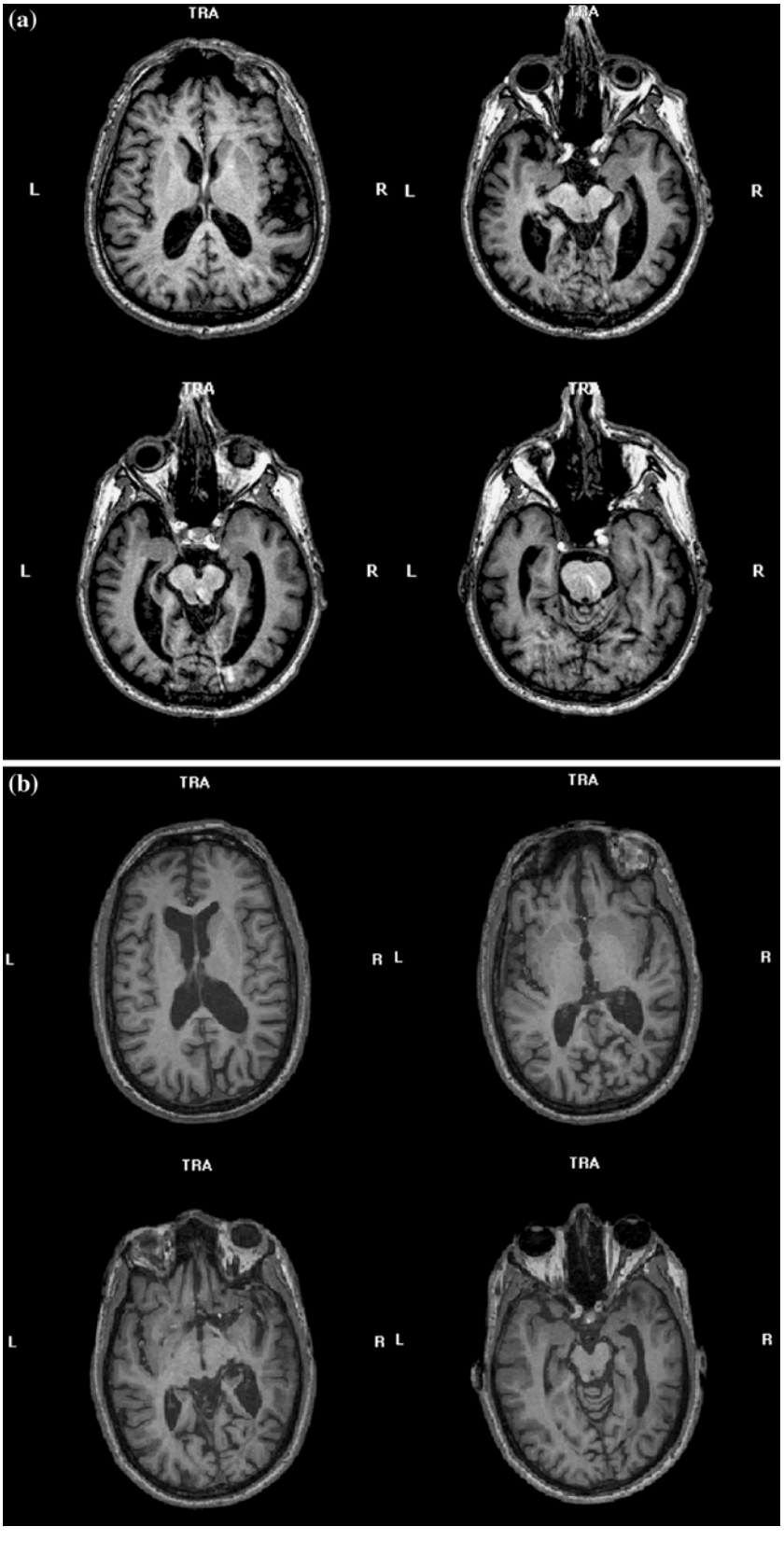

Fig. 1 Structural MRI scans for acquired prosopagnosic patients **a** AP1 (RN) **b** AP2 (SM). Scans were taken soon after behavioral testing, and several years post-onset for both individuals. See text for description of lesions

had normal or corrected-to-normal visual acuity by self-report. Community volunteers were paid for their participation, and students participated in return for course credit.

General methods

Participants were tested individually. Computer tasks (all tasks except famous face recognition and the Benton face recognition task) were run on a Dell laptop PC using E-Prime 1.1 (Psychology Software Tools, Inc.), at a viewing distance of approximately 60 cm. Stimuli remained on the screen until the participant made his or her response.

Face identity discrimination and recognition

To confirm that the prosopagnosic participants were impaired at face processing, we administered a famous face recognition task and an unfamiliar face discrimination task[2] to each individual and to the control individuals. The Benton Face Recognition Test was also administered to all CP and AP participants, although it should be noted that it is possible for prosopagnosic individuals to score in the normal range on this task (e.g. Duchaine and Nakayama 2004, 2006b). A further face discrimination (1-back) task was administered to the CP individuals and their matched controls (see Avidan et al. 2005).

We first compared the performance of CP, AP and control participants at recognizing famous faces. Fifty-six photographs of US celebrities were randomly intermixed with 56 images of unfamiliar faces (foreign celebrities). All images were taken from the internet and were cropped with a standard black oval to remove non-facial cues (see Fig. 2a for some examples). Roughly half the faces were male and half female, and the number of Caucasian and non-Caucasian faces was equated across the familiar and unfamiliar sets. The faces were presented in the form of a questionnaire with unlimited time to respond. A response giving either the name of the individual (e.g. Ronald Reagan) or contextual information (e.g. ex-President) was scored as correct. Other possible responses were an incorrect name or 'do not know' (see also Behrmann et al. 2005a). The results are displayed in Fig. 2b. Individual percentage correct scores were compared to the control mean (85.12%, $N = 30$) and scores more than two standard deviations below the control mean (i.e. below 56.28%) were considered atypical. Both AP individuals were impaired. CP1 and CP3 were also impaired. Although CP2 (62.5%) was just within the normal range, he scored well below his two age- and gender-matched controls, who averaged 93.75% correct.

The next experiment investigated performance on a same/different discrimination task with a pair of simultaneously presented grayscale faces (see Fig. 3a for examples). The members of each face pair differed at either the gender level (between category—30 trials) or individual level (same gender, different individuals; within category—30 trials) or were identical (40 trials) (see Gauthier et al. 1999 and Behrmann et al. 2005a for further details of this task). The results are displayed in Fig. 3b.

Again, accuracy or reaction times outside two standard deviations from the control mean ($N = 30$) were

[2] Note that the data on the CP individuals on these tasks are also presented in Behrmann et al. (2005).

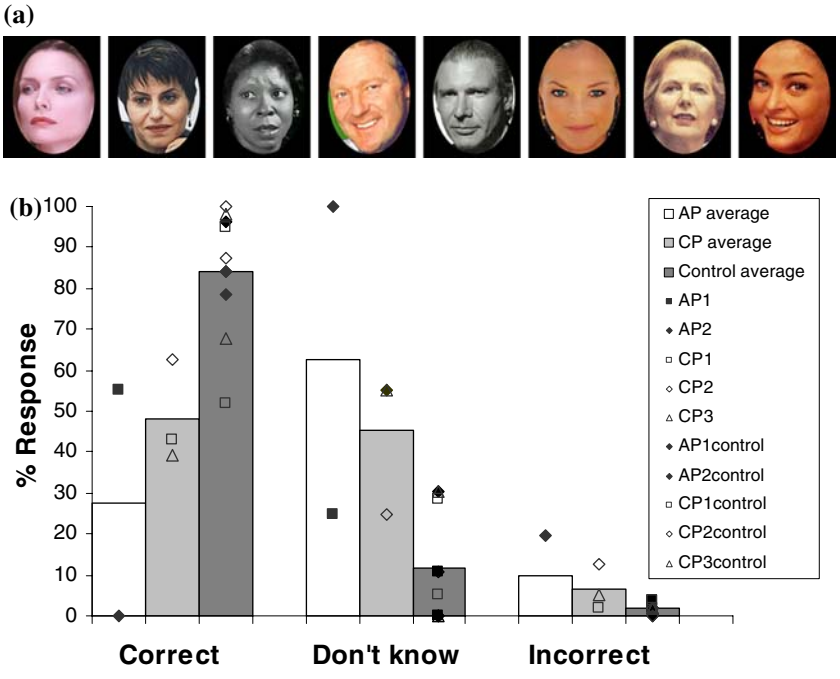

Fig. 2 **a** Example stimuli for famous face recognition and **b** famous face identification accuracy for APs, CPs and controls

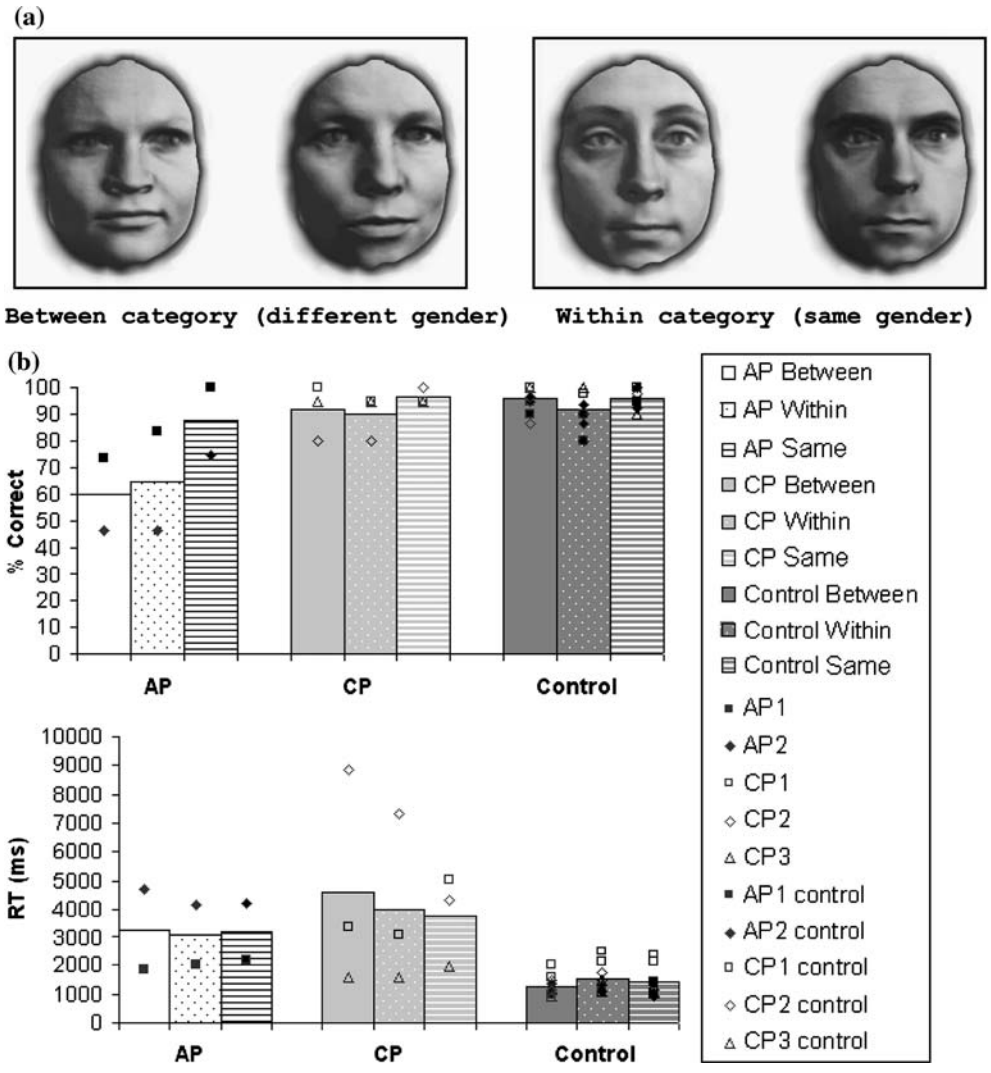

Fig. 3 **a** Example stimuli for unfamiliar face discrimination (two conditions: between category, in which the faces to be discriminated were of different genders, and within category in which both faces in the pair were of the same gender) and **b** unfamiliar face discrimination accuracy and reaction times for APs, CPs and controls

considered atypical. AP1 was inaccurate at between category discrimination and AP2 at both within and between category discrimination. AP2, but not AP1, also fell more than two standard deviations below the control mean in terms of d′, and AP2 was also atypically slow in both conditions. CP1, CP2 and CP3 were within normal accuracy limits, in terms of both accuracy and d′. CP1 and CP2 were atypically slow to respond in both conditions (within and between category). CP3 was in the normal range on this task (but, as above, was considerably slower than his own matched controls).

The Benton Face Recognition Test, a standard neuropsychological test in which a face identity must be matched across photographs varying in viewpoint and lighting, was administered to all the prosopagnosics. On this test, CP1 and CP2 were within normal range, with CP3 and AP2 severely impaired and AP1 borderline. Note that it is well established that normal scores on this task do not rule out difficulties with face processing (see Duchaine and Nakayama 2006b).

The CP, but not AP, individuals were tested on a sequential discrimination (1-back) task with line drawings of faces (Avidan et al. 2005). Stimuli were presented for 800 ms with a 200 ms inter-stimulus interval, and participants fixated centrally while detecting immediate repetitions. Even on this very simple task, CP1 and CP3 were below two standard deviations from mean control accuracy, with CP2 in the normal range (all three CP individuals were within normal reaction time limits).

Table 1 summarizes performance across the face identity tasks. Although not all individuals were impaired on all tasks (see e.g. Duchaine and Nakayama

Table 1 Summary of performance at face recognition and discrimination, and on the Benton face recognition task, for the AP and CP participants

Participant	Famous face recognition	Simultaneous face discrimination accuracy	Simultaneous face discrimination speed	Sequential face discrimination accuracy	Sequential face discrimination speed	Benton face recognition score
AP1	Borderline (55%)	Impaired (78%)	Normal (1,946 ms)	N/A	N/A	Borderline (40)
AP2	Impaired (0%)	Impaired (47%)	Impaired (4,578 ms)	N/A	N/A	Severely impaired (36)
CP1	Impaired (43%)	Normal (97%)	Impaired (3,275 ms)	Impaired (71%)	Normal (635 ms)	Normal (44)
CP2	Normal (62.5%)	Impaired (80%)	Impaired (8,080 ms)	Normal (100%)	Normal (639 ms)	Normal (43)
CP3	Impaired (39%)	Normal (95%)	Normal (1,579 ms)	Impaired (57%)	Normal (576 ms)	Severely impaired (32)

2006b, for discussion of this point, also Harris et al. 2005, Le Grand et al. 2006), taken together, the results indicate that all AP and CP individuals were impaired at processing face identity on many of them, either in accuracy or in RT. AP2 is clearly the most severely affected of the five, but, crucially, the impairments between AP1 and the CP individuals appear fairly similar in severity.

Facial expression recognition

Having confirmed that the facial identity processing of the CP (and AP) individuals is impaired, we then went on to investigate their facial expression processing, using a very fine-grained task, covering all six basic facial expressions (anger, disgust, fear, happiness, sadness, surprise), and incorporating both unambiguous and more subtle expressions. Specifically, morphed expressions from all possible pairwise combinations of the Ekman and Friesen (1976) six basic facial expressions were used. These stimuli have been widely used in previous research with other brain injured populations (e.g. Calder et al. 1996, 2000; Sprengelmeyer et al. 1996), and have been shown to serve as a very sensitive test of expression recognition. The stimuli were presented individually in a random order for a six-alternative forced-choice recognition response.

Stimuli

Stimuli were taken from the Facial Expressions of Emotion: Stimuli and Test (FEEST) (Young et al. 2002) set of morphed facial expressions. See Fig. 4 for an example.

Further details of the stimuli can be found in Young et al. (1997). Briefly, grayscale photographs of face JJ (Ekman and Friesen 1976) showing happiness, surprise, fear, sadness, disgust and anger, were morphed in all possible pair wise combinations (15 combinations). The proportions of the blend in each continuum were 90:10, 70:30, 50:50, 30:70 and 10:90 (e.g. 90% fear, 10% surprise, etc. for the fear-surprise continuum). Each continuum is labeled by the emotions at each end: fear-surprise is FS and then the proportion of the second emotion is included (FS10 indicates 10% surprise which implies 90% fear. The other expressions are abbreviated as follows: Anger, A; Disgust, D; Happiness, H; Sadness, M). The prototype (100%) expressions were not used. Neutral faces were also not included in the set as they are actually perceived as cold and threatening (Phillips et al. 1997), and their inclusion in the stimulus set appears to make no difference to the final results (Young et al. 1997). Thus there were 15 different continua, each consisting of five images, i.e. 75 faces in total. Each morphed face measured 11.4 cm horizontally and 14 cm vertically.

Procedure

The 75 morphed facial expressions were presented individually in the center of the screen in a random order. The task was to decide whether each image was

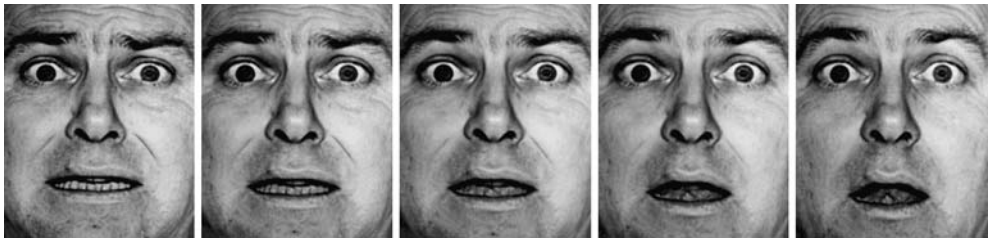

Fig. 4 Example of the fear-surprise continuum

most like happiness, surprise, fear, sadness, disgust or anger. Responses were made using six labeled keys on the keyboard in a pseudorandom order for each participant. No feedback was given as to the accuracy of the response. There were seven practice trials, and following this, 11 blocks of 75 test trials each. The task took between 25 min and 1 h.

Results

We first discuss the accuracy and reaction times for the unambiguous expressions (those which contained 90% of a particular expression). For each expression, results were obtained by pooling over all five stimuli containing that 90% expression (e.g. the 'happiness' results are the average of 90% happiness mixed with each of 10% fear, sadness, disgust, surprise and anger). We also present confusability matrices for these expressions. We then turn to all 75 expression blends to examine responses to the graded expression trials. In all cases, results falling outside two standard deviations from the control mean (calculated from the 30 control adults) were considered atypical.

Recognition of unambiguous expressions

We averaged responses across all trials for which the major expression strength was 90%, to investigate the degree to which prosopagnosics were able to identify unambiguous (90%) expressions. Mean accuracy and log reaction times[3] for the prosopagnosics and age and gender matched controls are shown in Fig. 5.

All CP individuals were well within two standard deviations of speed and accuracy limits for recognizing all six unambiguous expressions. In contrast, both AP individuals were markedly impaired, particularly at recognizing anger, disgust and sadness, with AP2 the more severely affected (and additionally impaired at recognizing fear). Both AP individuals were also slow to recognize all expressions with the exception of sadness, for which AP1 was borderline. Table 2 shows the confusability matrices for the AP individuals and the control average. Both AP individuals commonly misidentified anger as surprise or disgust, and sadness as disgust, as well as making other individual errors.

In contrast, all three CP participants showed a very similar pattern to that of the controls, with low misidentification rates. Where misidentifications were made, the most common confusions were that fear was occasionally misidentified as surprise, anger as disgust,

[3] Log reaction times were used here, but not for the identity tasks, to deal with the increased number of outliers for all groups, due to the length of the task (approximately five times longer than the identity task). This was thought preferable to excluding these data completely.

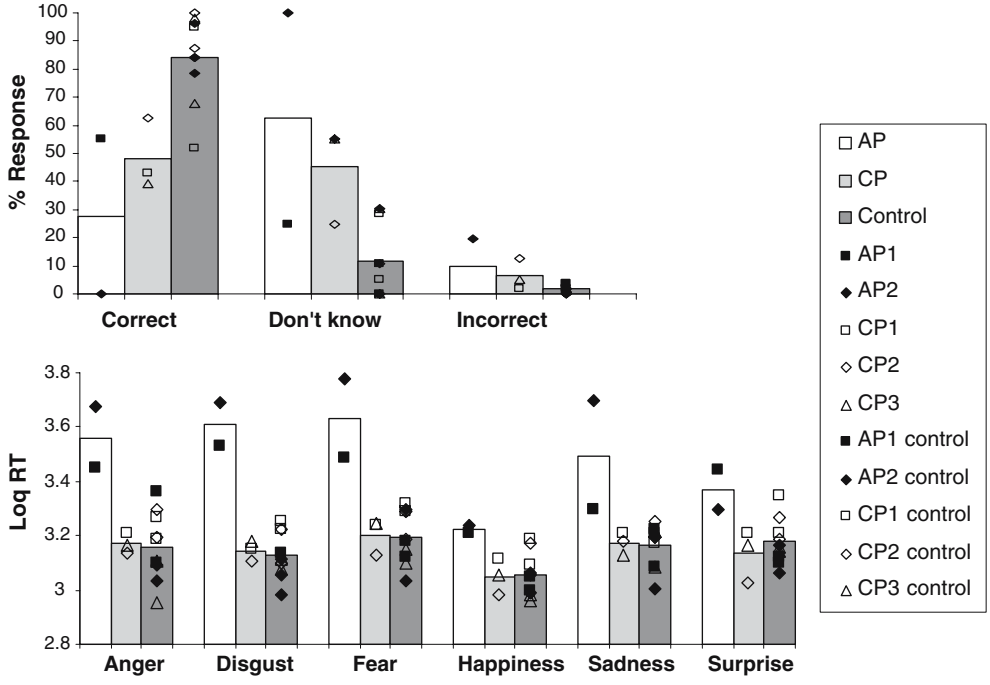

Fig. 5 Unambiguous (90%) expression recognition accuracy and log reaction times for acquired and congenital prosopagnosics and controls

Table 2 Confusability matrices (strong expression in image versus percentage of each response type made) for the two AP and three CP participants and an average of 30 controls

Image	Response					
	Anger	Disgust	Fear	Happiness	Sadness	Surprise
AP1						
Anger	56.36	14.55	3.64			25.45
Disgust	76.36	16.36			7.27	
Fear			98.18			1.82
Happiness				98.18		1.82
Sadness		25.45			74.55	
Surprise		1.82	10.91			87.27
Total	132.73	58.18	112.73	98.18	81.82	116.36
AP2						
Anger	25.45	23.64	12.73			38.18
Disgust	12.73	34.55	0.00	27.27	21.82	3.64
Fear	3.64		3.64	38.18		54.55
Happiness				100.00		
Sadness	7.27	40.00		9.09	36.36	7.27
Surprise		1.82	7.27			90.91
Total	49.09	100.00	23.64	174.55	58.18	194.55
CP1						
Anger	98.18					1.82
Disgust		100.00				
Fear	1.82	1.82	96.36			
Happiness				100.00		
Sadness	1.82				98.18	
Surprise			5.45		1.82	92.73
Total	101.82	101.82	101.82	100.00	100.00	94.55
CP2						
Anger	92.73	3.64	3.64			
Disgust	20.00	80.00				
Fear	1.82		98.18			
Happiness				100.00		
Sadness					100.00	
Surprise			1.82			98.18
Total	114.55	83.64	103.64	100.00	100.00	98.18
CP3						
Anger	98.18		1.82			
Disgust		100.00				
Fear	1.82		87.27			10.91
Happiness				100.00		
Sadness		3.64			96.36	
Surprise			3.64			96.36
Total	100.00	103.64	92.73	100.00	96.36	107.27
Mean of 30 controls						
Anger	96.36	1.33	0.67	0.12	0.24	1.27
Disgust	10.67	87.70	0.18	0.06	1.27	0.12
Fear	2.67	0.18	91.94	0.36	0.30	4.55
Happiness	0.06	0.12		99.39	0.24	0.18
Sadness	0.24	1.39	0.30		98.06	
Surprise		0.36	3.33	0.12	0.30	95.88
Total	110.00	91.09	96.42	100.06	100.42	102.00

fear or sadness and disgust as sadness or anger. These are similar to the confusions made by the controls tested here, and in previous reports (Young et al. 1997). To attempt to bring CP and control performance off ceiling, and because this is standard practice in some earlier publications using these stimuli, we also compared these two groups on performance averaged across the 90 and 70% expressions, and again the groups were indistinguishable (see Appendix).

Recognition of all expression morphs

From the analyses above, we have seen that, with unambiguous expressions, the AP participants were markedly impaired, whereas the individuals with CP performed like the normal controls. However, it is possible that this reflected a ceiling effect for the CP group (even with the 90 and 70% results averaged, accuracy was still very high) and that with more subtle expressions, differences

between the CP group and controls would become apparent. Previous studies have also shown that testing expression recognition with prototypical expressions alone can provide an underestimate of the extent of an individual's difficulties. For example Adolphs et al. (1995) found that their bilateral amygdala patient, SM, showed more widespread difficulties with expression recognition, affecting judgments of anger, fear and surprise, on a subtle test with different intensities of expressions, than she did when tested prototypical expressions, the results of which misleadingly suggested that her deficit was limited to fear recognition. Thus, we were interested to see how the CP participants performed with this, more sensitive, test.

Figure 6 shows the percentages of each of the six responses (anger, disgust, fear, happiness, sadness, surprise) to each of the 75 facial expression morphs, for a representative control and each CP and AP participant.

Previous studies (e.g. Young et al. 1997) have shown that neurologically normal participants typically perceive these morphed expressions as falling into six distinct categories (corresponding to the six basic expressions) with sharp boundaries between them, such that, for example, morphs between happiness and sadness will be perceived as happiness up to a certain point along the continuum, and then will shift to being consistently perceived as sadness. As is evident from Fig. 6a showing data from a typical control, the control responses replicate this expected pattern.

As was the case for the unambiguous expressions, performance of the CP participants was indistinguishable from that of controls even with these subtle expression blends; both groups showed similar peaks and troughs for each of the expression responses and the functions are clean and repeatable across all expressions. The fact that the CP individuals performed so much like the controls certainly cannot be explained by a lack of sensitivity of this experiment as the AP individuals exhibited marked deviations from the control response pattern, for all expressions except happiness and surprise. For example, responses for AP1 to the disgust-anger continuum show no clear shift from consistent "disgust" to consistent "anger" judgments, as the degree of "anger" in the stimulus increases, as did the responses of controls or the CP participants; instead, AP1 responded "anger" on approximately 70% of trials and "disgust" on approximately 30% of trials across the entire disgust- continuum, with little change in response rates with the change of the degree of "anger" in the stimulus.

As a means of summarizing the entire pattern, we calculated the number of times (out of 450: 75 images × 6 possible responses) that each prosopagnosic individual fell outside the normal response limits.[4]

AP1 fell outside normal response limits (two standard deviations from the control mean) for 20% of the image-response combinations, and AP2 did so on 35% of the combinations. In contrast, CP1 was outside these limits for only 3.5% image-response combinations, CP2 2% and CP3 3.5% and a randomly selected control, 5%; these low levels of apparent errors appear inevitable with so many comparisons, and can be caused by occasional incorrectly triggered key strokes, for example. Reaction time data were not analyzed for the full set of expression morphs because of the number of missing cells and the low numbers of responses which contributed to the data points in many cases (e.g. it was very rare for 'sad' responses to be made to a 'happy' face).

Discussion

The performance of all three CP individuals at discriminating both unambiguous and more subtle expression blends was indistinguishable from that of controls. We do not believe that this reflects a ceiling effect because there was no marked difference between the CP individuals and controls even for more subtle expressions. The performance of the CP individuals stands in stark contrast to that of both AP patients, despite the somewhat similar levels of identity impairment between AP1 and the CP participants. Both AP participants were highly impaired at expression recognition, with AP2 appearing to be, broadly speaking, a more impaired version of AP1 both in identity and expression processing. The only expressions accurately recognized by both AP individuals, albeit slowly, were happiness and surprise.[5]

General discussion

The aim of this investigation was to provide a detailed investigation of facial expression processing

[4] An analysis based on *z*-scores, such as this, is not strictly speaking, appropriate, as in many cases (e.g. sadness responses to an expression of happiness), there was very little variation in the control group data, and, certainly they were not normally distributed. However, in this subsidiary analysis, we wished merely to give an indication of the relative numbers of 'atypical' responses for the CP and AP individuals.

[5] It should be noted that this accuracy for happiness was not a criterion bias, as neither participant had a tendency to answer 'happy' for the other stimuli, although for surprise this may have been so (particularly in the case of AP2, who answered 'surprise' approximately twice as often as normal).

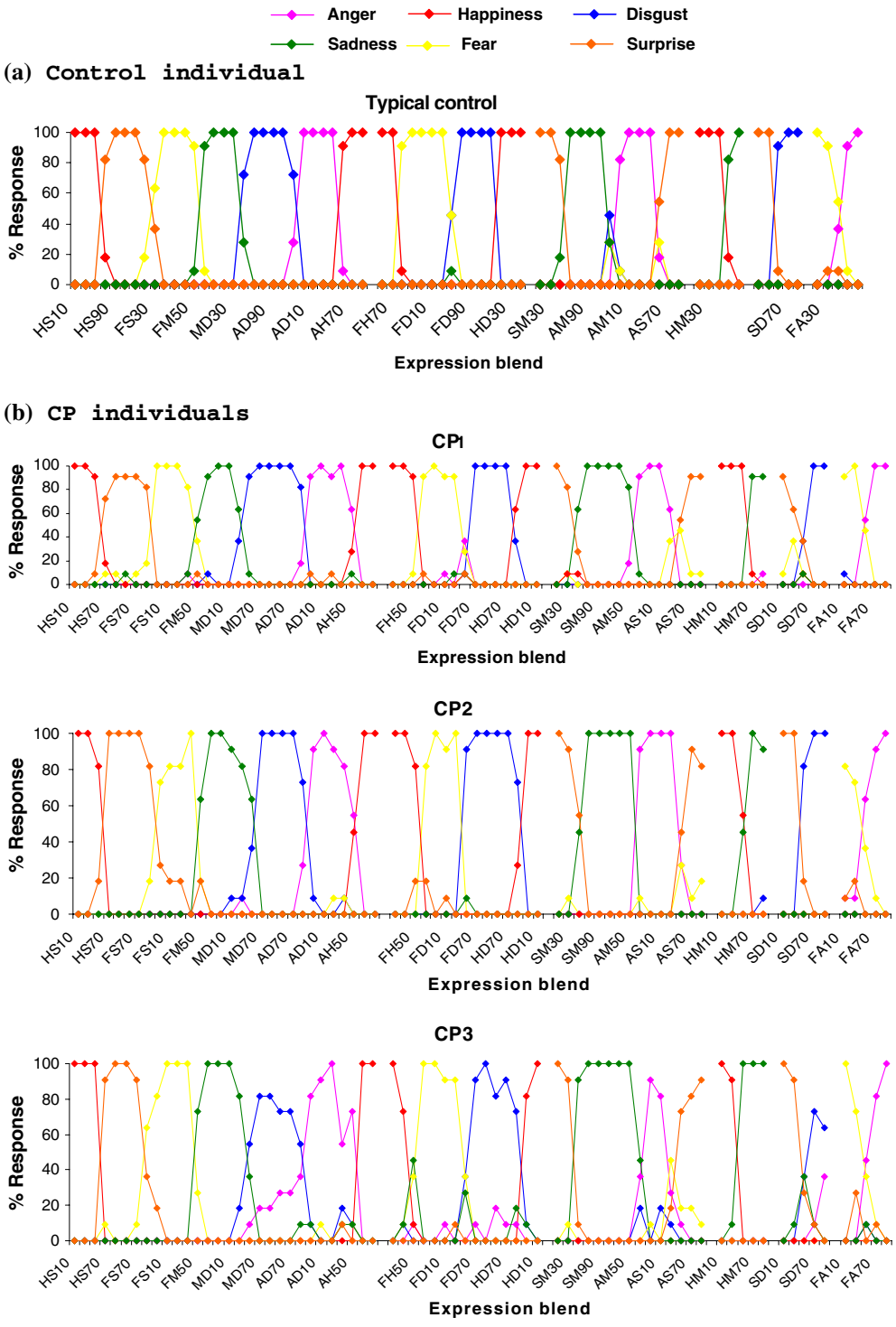

Fig. 6 Mean percentage anger, disgust, fear, happiness, sadness and surprise responses for **a** a representative control and each of the three **b** CP and **c** AP participants

in a small group of adults with congenital prosopagnosia (CP), carefully selected to have no coexisting psychological or neurological pathology. Specifically, demonstrating that facial expression recognition can be dissociable from facial identity recognition is important from a theoretical point of view and speaks to the potential independence of these forms of visual processing, as proposed by many major models of face processing (for example, Bruce and Young 1986; Haxby et al. 2000). Documenting the nature of facial expression processing in CP is also valuable in the context of providing a full and

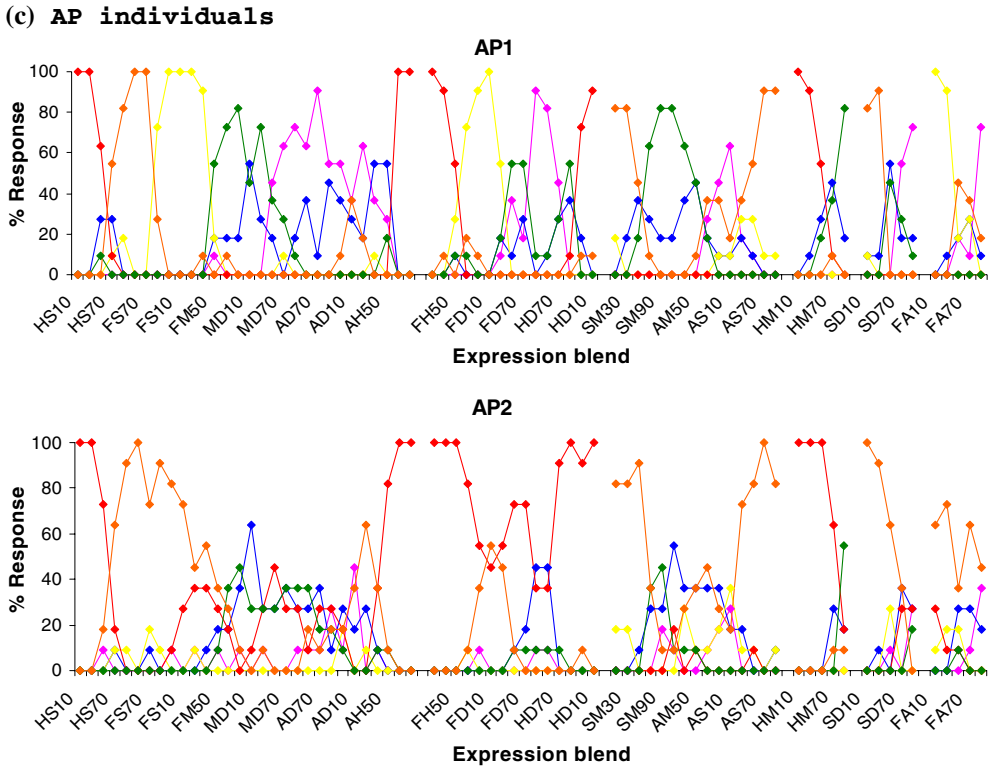

Fig. 6 continued

complete description of the visuoperceptual abilities of CP individuals especially since this type of disorder is receiving increasingly close scrutiny in the literature (Behrmann and Avidan 2005).

Although there have been some previous reports of preserved facial expression processing in CP, these are few in number, have mostly employed different methods and have been mostly single case studies. In this study, we utilized a fine-grained paradigm with which we documented the expression recognition of the six basic expressions as well as subtle versions of these expressions, in terms of accuracy, sensitivity and reaction time. The results of the CP individuals were compared with both those of a large neurologically normal population (amongst which were individually matched controls for the CP participants) and with two individuals with AP, one of whom had similar levels of identity difficulties to the CP group.

The findings from these experiments were striking. The performance of the CP individuals in discriminating facial expressions was homogeneous within the group, and, importantly, indistinguishable from that of controls, even using methods and measures sensitive enough to discern subtle deficits (both reaction time and accuracy measures). Note that the parallel patterns between the controls and CP individuals were evident both for strong versions of the expressions as well as for more subtle instances of the images, as reflected in the morphed or blended images. The failure to find any difference between the CP and the normal control group cannot be attributed to a lack of sensitivity of the measuring instruments. In marked contrast to the CP individuals, on the very same tests, the performance of both AP patients was severely impaired, despite the fact that one of them was similar to the CP participants on identity processing tasks. The apparent null result for CP individuals, therefore, clearly cannot be explained by a lack of power as the experiment uncovers deficits in those with AP.

Our finding that all three CP participants were unimpaired at expression recognition, even with the most subtle expression blends, is consistent with the single-case study of a CP individual by Duchaine et al. (2003a), and with the other reports of no impairment in CP (Bentin et al. 1999; Jones and Tranel 2001; Kress and Daum 2003b; Nunn et al. 2001). It appears to contrast with the studies reporting expression deficits (Ariel and Sadeh 1996; Campbell 1992; Duchaine et al. 2003b, 2004; Kracke 1994). As discussed in the introduction, however, there is some question as to whether the individuals in these latter studies suffered from co-existing neurological or social difficulties that might, in themselves, have accounted for the facial expression recognition difficulties. It is to be noted that, unlike

some previous studies, we used very strict criteria for inclusion in our sample excluding anyone with any suspicion of social or neurological abnormalities. We were particularly mindful to exclude anyone with a possible autism spectrum disorder. Our contribution is to extend previous findings of normal expression recognition performance in CP to a larger, more strictly defined, group than has been done previously.

A number of important issues remain. One issue concerns the generalizability of our results to all cases of CP. A second issue concerns the mechanism for preserved facial expression processing in CP and a final, related, and perhaps most central question concerns the implications of the findings for theories of dissociable facial expression and identity processing. We take each of these in turn.

Do the results generalize to all cases of CP?

The present results, and our review of the literature, might appear to suggest that facial expression processing performance is at normal levels in all pure cases of CP. However, this might not necessarily be the case. Certainly CP individuals may be found in the future who have difficulties with expression processing, and it would be premature to characterize CP as a disorder in which identity processing is impaired but facial expressions are always well recognized. We further note that the CP participants tested here were not homogeneous with respect to other types of visuoperceptual processing; all three took part in tests of facial gender and familiar and unfamiliar object recognition (not reported here). They showed a mixed pattern of results on these tasks, from no deficits at one extreme, to deficits on all three tasks at the other (see Behrmann et al. 2005a for the object recognition results). These findings speak against the homogeneity of CPs as a group (see also Harris et al. 2005; Le Grand et al. 2006), and thus we have no reason to suspect that as a group they are perfectly homogeneous with respect to facial expression processing. Indeed, only time and further investigations that address the separability of facial identity and expression processing in CP will attest to the generalizability of the results we have reported. Given the increase in interest in CP and the flurry of recent papers on the topic, indications of a general pattern, if one exists, will surely be uncovered.

Why do CP individuals have preserved expression processing?

The question arises as to how our participants with CP recognize facial expressions so well. Broadly speaking, it would appear that there are five possible explanations. The first is that facial expressions and identity are processed by the same mechanism, but that expressions are simply 'easier' (Calder and Young 2005), at least with the tasks we used here, and thus are less affected by any disruption to the mechanism. We do not believe that this is likely to be the explanation, since one of our AP participants showed broadly similar identity recognition deficits to the CP participants, yet was severely impaired at perceiving facial expressions (although the AP and CP participants were not perfectly matched in terms of their face identity performance). Furthermore, control accuracy at recognizing famous faces and recognizing strong facial expressions (90 or 70%—see Appendix) did not differ significantly when compared in a t test [$t(9) = 1.805$, $P = 0.105$], suggesting that the tasks for identity and expressions were approximately matched in difficulty. However, we would like to point out that one of the major limiting factors of research identifying dissociations between identity and expression recognition, including the present research, is that studies have failed to compare like with like. Tasks assessing facial expression recognition have tended to used matching or forced-choice selection procedures (with a small number of response options). In contrast, facial identity recognition is typically assessed by asking participants to identify a series of famous faces. Certainly, future studies would be well advised to use faces morphed between different facial identities and those morphed between different expressions, with the difficulty levels of the two tasks titrated to be matched in the normal population.

The second explanation is that the mechanisms that give rise to CP do not disrupt the neural substrates that would typically support facial expression processing, and would thus allow facial expression processing mechanisms to develop normally, and independently of the impaired identity processing. This view favors the independence of identity and expression processing and would be consistent with the accounts of functional and neural separation, espoused by Bruce and Young (1986) and by Haxby et al. (2000), respectively. In contrast, the AP individuals have relatively widespread damage, which may well include areas that have been implicated in facial expression recognition (including the superior temporal sulcus and parietal cortex in the case of RN, whose lesion includes bilateral parieto-temporal areas), and anterior temporal lobe and basal ganglia (in the case of SM).

A third possibility is that neural substrates that would typically support expression processing mechanisms are disrupted in these CP cases, but that there is plasticity in the brain for expression processing (unlike

identity processing), so that a computationally 'normal' expression processing system arises in an atypical brain location. This model may, but does not necessarily, support a distinction between systems for identity and for expression processing (both could be affected independently in CP although this is less parsimonious than a single mechanism account), and suggests that, after any form of alteration that affects both systems, one can circumvent the latter but not the former deficit. The fourth possibility is an alternative version of the third one. As above, the claim is that in CP the neural substrates that would typically support expression processing are disrupted (along with identity disruption) but that there is no plasticity for 'normal' expression processing to develop elsewhere in the brain; however, with a lifetime of experience with facial expressions, individuals with CP have developed compensatory strategies for expression recognition, and have become quite expert in their use to the degree where they can achieve normal levels of performance (see Karmiloff-Smith 1997 for a pertinent discussion). There are only a small number of facial expressions (unlike facial identities), and it is certainly plausible that the six basic facial expressions could be recognized using distinctive facial features alone, such as a smiling mouth for happiness. However, we believe that any such compensatory mechanisms would have to be very sophisticated to have exactly replicated the normal pattern of performance even with the subtle, and artificial, blends of expressions presented in the current investigation.

Finally, it is possible that these data are consistent with the position recently suggested by Calder and Young (2005). These authors suggested that the visual representations of facial identity and expression are coded by a single system, but that, within this system there is a partial (statistical) dissociation between the identity and expression codes (and, of course, there is separation of non-visual identity and expression processing). A congenital disorder might produce a disproportionate deficit in facial identity recognition if that code relies on a particular type of information that the disorder disrupts, and which is less involved in facial expression recognition. For example, configural information may be more important for identity than expression. Similarly, disrupted texture information (or shape from shading) can have a dramatic effect on identity recognition but it is not clear whether the same applies to facial expressions.

To date, it is not possible to distinguish between these possibilities. Future studies could investigate whether CP individuals process expressions using atypical, possibly compensatory, processes, by employing techniques such as eye-tracking, or 'Bubbles' (Gosselin and Schyns 2001) or by manipulating the degree to which more typical, 'holistic' processing can be employed with facial expression stimuli and monitoring the effect of this manipulation on CP individuals versus controls (see Bukach et al. 2006; Caldara et al. 2005, for studies in this vein addressing identity processing in AP). Neuroimaging studies could also potentially determine whether the neural substrates supporting face processing in CP differ from those in controls and some such studies have already started to appear (Avidan et al. 2005; Hasson et al. 2003; von Kriegstein et al. 2006).

The theoretical implications of dissociable identity and expression impairments

As set out in the introduction, there remains an ongoing controversy regarding the separability of visuoperceptual mechanisms mediating facial identity and facial expression processing. While models espousing the independence of systems for identity and expression have garnered much support, there are data that challenge the separability claim. For example, Ganel et al. (2005) have shown that the BOLD activation in the fusiform gyrus, which is typically associated with identity processing, is even more greatly activated for judgments of expression than of identity. When the single-cell recording data are examined in detail, they also fail to provide strong support for a separation between the coding of expression and identity (see Tiberghien et al. 2003). Behaviorally, there is evidence that varying identity information can interfere with the classification of expressions (Schweinberger et al. 1999), indicating that the two may not be fully independent. Additionally, as discussed above, Calder and Young (2005) have suggested that the apparent dissociation between identity and expression processing might be obtained from the partially independent visual coding of identity and expression within a single multidimensional visual coding system (see also Calder et al. 2001).

The data from the current investigation are easily interpretable in terms of the models claiming independence in that there is normal preservation of expression processing concurrent with fairly marked identity impairments. Calder and Young (2005), however, have argued for caution in extrapolating the findings from congenital prosopagnosia to the identity/expression debate. Their main argument is that developmental cases violate a fundamental assumption of the dissociation logic, namely that a brain injury affected a normally organized system (see also Bishop 1997; Karmiloff-Smith et al. 2003; Thomas and Karmiloff-

Smith 2002). Indeed, as we outlined above, an alternative explanation for the CP performance in the present study is in terms of atypical brain organization, specifically the atypical development of circumventory and/or compensatory mechanisms for facial expression processing. However, we would argue that this is too narrow a version of the dissociation logic and that the CP findings are valuable in this context, even if brain organization is atypical. Let us imagine for argument's sake that facial identity and expression are jointly subserved by the same system in the normal brain. The apparent preservation of expression processing in CP suggests that this form of perception is plastic and can be compensated for while identity cannot. In essence, this draws a distinction between identity and expression processing and speaks to their separability. Even if (in the worst theoretical case scenario) facial expression processing in CP relies on atypical, compensatory processing, the question remains why identity cannot be compensated for in the same way. As such, these data speak well to the distinction between identity and expression processing and have bearing on the ongoing debate. (It should be noted, however, that it remains a possibility that compensation for expression recognition is simply easier than for facial identity; there is only a small set of facial expressions whereas the set of possible facial identities is unconstrained.)

One final comment is necessary before concluding and that concerns the AP individuals. While our main focus here has been to explore facial expression processing in CP, the data from the AP patients are also interesting and worthy of some discussion. The finding that both AP participants were severely impaired at expression recognition is consistent with many other findings (Bowers et al. 1985; de Gelder et al. 2000; De Renzi and Di Pellegrino 1998; Humphreys et al. 1993) but extends these results to more detailed testing, and to individual results for the individual expressions, rather than treating them as a single entity. It stands in contrast to reports (e.g. Bruyer et al. 1983; Cole and Perez-Cruet 1964; Mattson et al. 2000; Sergent and Villemure 1989; Shuttleworth et al. 1982; Tranel et al. 1988; Young et al. 1993) of intact facial expression processing in AP. However, several points concerning these reports of intact facial expression processing should be noted. For the patient reported by Shuttleworth et al. (1982) there was no formal assessment of facial expression recognition and no data are presented; preserved performance is supported only by anecdote. Sergent and Villemure's (1989) patient was actually more than two SD outside the control range on a test of facial expression recognition. None of the patients reported by Young et al. (1993) was identified as having an impairment which was selectively worse for faces (one of the basic criteria for prosopagnosia), and the patient reported by Mattson et al. (2000) had impaired visual acuity and basic visual processing, and so does not qualify as prosopagnosic. It is not clear, then, whether there is *genuine* heterogeneity in the AP population with respect to expression processing (see Calder and Young 2005 for further discussion).

Conclusion

To summarize, our exploration of facial expression processing in a group of three CP individuals indicated that facial expression processing was at normal levels in all three, despite being grossly impaired in two comparison individuals with AP. Further studies are necessary to investigate the neural and computational mechanisms underlying this apparently 'spared' expression processing, and to uncover the mechanisms that enable facial expression to be well-preserved while facial identity processing is markedly impaired.

Naturally, this set of studies is subject to limitations. All the tests of identity and expression recognition presented here involved explicit recognition. Further, all tasks, except the Benton Facial Recognition Task, used frontal views of static faces. We note that different results might be obtained with different viewpoints or moving faces (see e.g. Humphreys et al. 1993, for evidence of a dissociation between results for moving and static expressions and O'Toole et al. 2002, for a discussion of movement in face recognition). Of course, collecting data from a larger group of CP individuals is also critical before any definitive conclusions about intact expression processing in CP can be reached.

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Appendix

Analysis of performance on the 70 and 90% expressions averaged together

Mean accuracy and log reaction times for the prosopagnosics and age and gender matched controls averaged across the 90 and 70% morphs are shown in Fig. 7. It can be seen that the pattern of results is highly similar to that for the 90% morphs alone (Fig. 5).

As in the analysis for the 90% morphs, results falling outside two standard deviations from the control mean

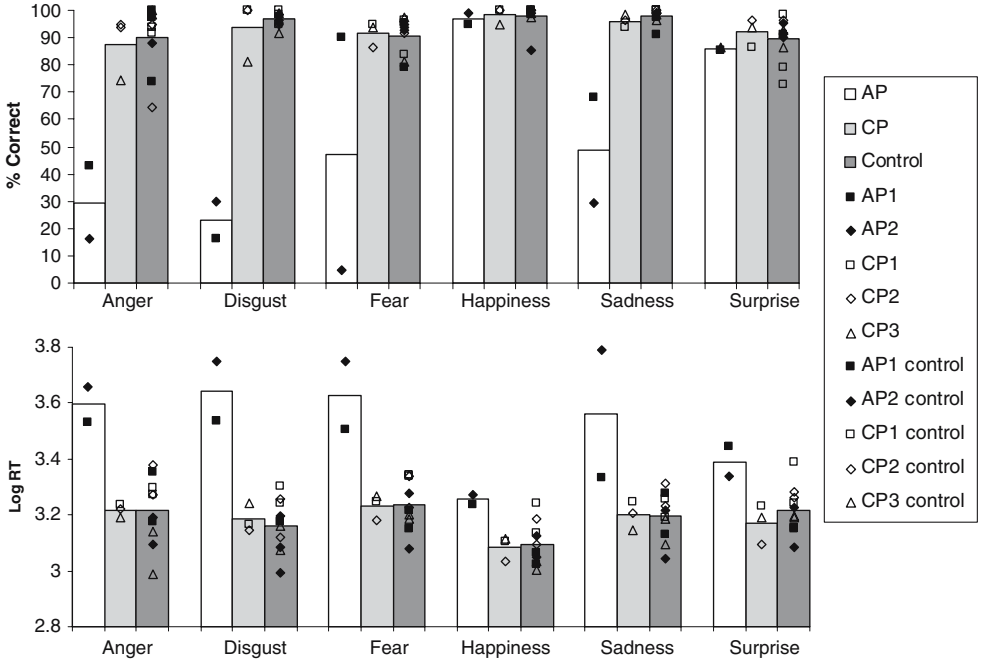

Fig. 7 Expression recognition accuracy and log reaction times averaged across the 70 and 90% expression blends for acquired and congenital prosopagnosics and controls

(calculated from the 30 control adults) were considered atypical. As in the main (90% only) analysis, all CP individuals were well within two standard deviations of speed and accuracy limits for recognizing all six unambiguous expressions. In contrast, both AP individuals fell outside these limits for accuracy at recognizing anger, disgust and sadness, with AP2 the more severely affected (and additionally impaired at recognizing fear). Both AP individuals were also slow to recognize all expressions with the exception of sadness, for which AP1 was just within normal limits.

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