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Research report

Evidence of an eye movement-based memory effect in congenital prosopagnosia

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ABSTRACT

While extensive work has examined the role of covert recognition in acquired prosopagnosia, little attention has been directed to this process in the congenital form of the disorder. Indeed, evidence of covert recognition has only been demonstrated in one congenital case in which autonomic measures provided evidence of recognition [Jones RD and Tranel D. Severe developmental prosopagnosia in a child with superior intellect. Journal of Clinical and Experimental Neuropsychology, 23: 265–273, 2001], whereas two investigations using behavioural indicators failed to demonstrate the effect [de Haan EH and Campbell R. A fifteen year follow-up of a case of developmental prosopagnosia. Cortex, 27: 489–509, 1991; Bentin S, Deouell LY, and Soroker N. Selective visual streaming in face recognition: evidence from developmental prosopagnosia. Neuroreport, 10: 823–827, 1999]. In this paper, we use a behavioural indicator, an ''eye movement-based memory effect'' [Althoff RR and Cohen NJ. Eye-movement-based memory effect: a reprocessing effect in face perception. Journal of Experimental Psychology: Learning, Memory and Cognition, 25: 997–1010, 1999], to provide evidence of covert recognition in congenital prosopagnosia. In an initial experiment, we examined viewing strategies elicited to famous and novel faces in control participants, and found fewer fixations and reduced regional sampling for famous compared to novel faces. In a second experiment, we examined the same processes in a patient with congenital prosopagnosia (AA), and found some evidence of an eye movement-based memory effect regardless of his recognition accuracy. Finally, we examined whether a difference in scanning strategy was evident for those famous faces AA failed to explicitly recognise, and again found evidence of reduced sampling for famous faces. We use these findings to (a) provide evidence of intact structural representations in a case of congenital prosopagnosia, and (b) to suggest that covert recognition can be demonstrated using behavioural indicators in this disorder.

Previous work has reported an eye movement-based memory effect in the viewing of familiar compared to novel stimuli (Althoff et al., 1998; Althoff and Cohen, 1999; Barton et al., 2006). This ''reprocessing effect'' is characterised by fewer fixations and the sampling of fewer regions in repeated items, and has been documented in the viewing of scenes (Ryan

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et al., 2000) and famous faces (Althoff et al., 1998; Althoff and Cohen, 1999; Barton et al., in press). Evidence of the eye movement-based memory effect has also been reported in amnesic patients who were asked to view scenes (Ryan et al., 2000) and to recognise familiar faces (Althoff, 1999). Given this evidence of covert recognition, it is pertinent to ask whether the effect can be extended to prosopagnosic patients in the viewing of faces. An extensive literature exists concerning the role of covert processing in acquired prosopagnosia, yet little work has investigated such processes in its congenital equivalent. However, it has been suggested that covert recognition can only be found on autonomic and not behavioural indicators in this condition (Kress and Daum, 2003). In this paper we provide evidence against this claim, and show that covert recognition can be demonstrated in a case of congenital prosopagnosia using measures of the visual scanpath.

Although prosopagnosia is more commonly reported following an acquired brain injury, there has been growing interest in people who suffer from face recognition deficits from birth (Ariel and Sadeh, 1996; Avidan et al., 2005; Behrmann and Avidan, 2005; Behrmann et al., 2005; Bentin et al., 1999; Campbell, 1992; de Gelder and Rouw, 2000; de Haan, 1999; de Haan and Campbell, 1991; Duchaine, 2000; Duchaine et al., 2003a, 2004; Duchaine et al., in press; Galaburda and Duchaine, 2003; Jones and Tranel, 2001; McConachie, 1976; Nunn et al., 2001). This condition has been referred to as 'congenital prosopagnosia', and is characterised by a face processing impairment that has been present from birth, in the context of intact visual and intellectual functions and in the absence of any neurological damage (Jones and Tranel, 2001). Some case studies have reported a familial connection in congenital prosopagnosia (Behrmann et al., 2005; Bentin et al., 1999; de Haan, 1999; Duchaine, 2000; Duchaine et al., 2003b; Kracke, 1994; McConachie, 1976), and a recent study suggests there is a genetic basis for the disorder (Grüeter et al., in press). The condition is therefore distinguished from the umbrella term 'developmental prosopagnosia', which is used when the condition results from neurological damage at any stage of development, visual deprivation such as infantile cataracts, or from other developmental problems such as autism.

The performance of individuals who present with congenital prosopagnosia is inconsistent, raising the possibility that the condition may not be a unitary disorder (Kress and Daum, 2003). Indeed, some perform relatively well in feature-matching tasks, yet reaction time is often slow and the impairment is revealed when task demands are increased (Kress and Daum, 2003). Similarly, mixed findings have emerged in tasks requiring recognition of famous faces. Some people with congenital prosopagnosia recognise very few, if any, famous faces (Bentin et al., 1999; de Gelder and Rouw, 2000), whereas others appear to show reasonably intact recognition abilities (Duchaine, 2000; Duchaine and Nakayama, 2005; Schwarzer et al., in press; Temple, 1992). Further, it is also unclear whether the same distinction can be applied across the apperceptive (an impairment in deriving an intact percept of a face) and associative (impairment at the level of semantics) subtypes as reported in acquired prosopagnosia (de Renzi et al., 1991). Indeed, the majority of congenital cases is present with a perceptual impairment, with only three cases in the literature apparently showing the associative form of the disorder (Dr S: Temple, 1992; BC: Duchaine, 2000; TA: Jones and Tranel, 2001).

This sub-classification is particularly important given evidence of a relationship between covert recognition and perceptual impairment. In acquired prosopagnosia, covert recognition has been demonstrated in virtually all patients with an associative impairment but only in some patients with an apperceptive impairment. This finding suggests that some residual capacity to encode face representations is required to demonstrate covert recognition. Some authors have argued against the existence of covert processing in congenital prosopagnosia, because this process relies on sub-threshold activation of previously intact face representations (e.g. Barton et al., 2001). Evidence in support of this statement is mixed. de Haan and Campbell (1991) and Bentin et al. (1999) failed to find evidence of covert recognition in their patients with congenital prosopagnosia (AB and YT) using behavioural measures. However, a recent study has demonstrated covert recognition in a case of congenital prosopagnosia using an autonomic measure (TA: Jones and Tranel, 2001). In this five-year-old boy, skin conductance responses were enhanced during presentations of familiar faces (family and close friends), despite his inability to name any of these people. In line with dual-route models of face recognition (e.g. Breen et al., 2000; Ellis and Lewis, 2001), it has been argued that covert processing can only be found using autonomic and not behavioural indicators in this condition (Kress and Daum, 2003). However, an alternative explanation may lie in the nature of the impairment in these patients. Importantly, AB and YT display perceptual impairments that would classify them as having an apperceptive form of the disorder, whereas TA is more representative of the associative form (see de Renzi et al., 1991). While it is not clear whether these two subtypes map onto congenital prosopagnosia in the same manner as they do in acquired prosopagnosia (Kress and Daum, 2003), it is nevertheless not surprising that behavioural tests of covert recognition did not reveal residual knowledge in AB and YT. According to this hypothesis, we would predict that TA (who presents with an associative impairment) would also show evidence of covert recognition on behavioural measures. Unfortunately, these data were not collected and it remains to be shown whether covert recognition can be demonstrated using behavioural measures in another case of associative congenital prosopagnosia.

The monitoring of eye movements provides another means to observe covert processing (Bruyer, 1991). Indeed, Althoff and colleagues (Althoff et al., 1998; Althoff and Cohen, 1999) present evidence of an eye movement-based memory effect as a means to discriminate between the viewing of famous and novel faces in healthy participants. In comparison to famous faces, the viewing of novel faces was characterised by more fixations, more regions (i.e. facial features) sampled, more fixations made before returning to a previously sampled region, and a greater proportion of fixations elicited to the left side of space and the inner features (i.e. eyes, nose and mouth). Further, these authors used first- and second-order Markov matrices to examine the sequential organization of scanning, and suggested that famous faces were associated with more random scanning sequences than novel faces.

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Barton et al. (2006) reported a similar distinction between the viewing of famous and novel faces using fixation-based measures (number of fixations and total dwell time), but could not replicate the finding using Markov matrices.

Various measures of the scanpath have been used to provide evidence of covert recognition in neurological patients. Rizzo et al. (1987) used first-order Markov matrices to provide evidence of covert recognition in two patients with acquired prosopagnosia, although they could not replicate this finding in their healthy control participants. Further, two studies have examined the eye movement-based memory effect in patients with amnesia. Ryan et al. (2000) noted a difference in the viewing strategies elicited to repeated and novel scenes in their patients with amnesia, characterised by reduced sampling (i.e. fewer fixations and fewer regions sampled) for repeated as compared to novel scenes. However, these patients were not asked to make a conscious recognition judgment, and it is possible they may have retained some explicit knowledge of the repeated scenes. Nevertheless, Althoff (1999) reported a difference in the viewing of learned (i.e. following a study phase) relative to novel faces in seven patients with amnesia, and found evidence for the effect even for those repeated faces that were not consciously recognised by the patients. This research suggests that the influence of previous exposure can be observed in visual processing independently of explicit remembering.

From the above discussion, it is apparent that some measures of the visual scanpath may be more reliable indicators of recognition than others. In the present research, we employed six measures in addition to the standard behavioural measures of accuracy and reaction time to examine the influence of familiarity on scanning strategy. Given the nature of this study, we selected variables that had particular theoretical value in understanding the information processing strategies relevant to recognising faces. There are further benefits of using eye-tracking in addition to standard behavioural measures in a study that examines face processing in prosopagnosia. Primarily, the presence of a response bias in the forced-choice decisions of neurological patients can obscure evidence of covert recognition. In prosopagnosia, a bias towards a 'novel' rather than 'familiar' decision is often reported, limiting the insight that can be drawn from accuracy on such a decision task. Use of other indicators can overcome this constraint. Second, the eye movement-based memory effect can reveal the nature of internal face representations (Barton et al., 2006). Specifically, in face identification, the goal of viewing is to match the present face to representations of familiar faces. What is not clear in prosopagnosia is whether the internal representations of faces are damaged or absent, or whether these representations are intact and it is the connections to other parts of the system that are impaired. The contrast between viewing patterns elicited to famous and novel faces may help to reveal the nature of these internal representations in the prosopagnosic case.

In the current series of studies we investigate the eye movement-based memory effect in healthy adults and a case of congenital prosopagnosia, AA. Experiment 1 essentially involved a replication of Althoff and Cohen's (1999) study, both to provide confirmation of the eye movement-based memory effect in healthy participants and to provide a control group for comparison with AA. In this study, we monitored the visual scanpath of healthy adults participating in a standard recognition task involving famous and novel faces. The aim of Experiment 2 was to investigate the same effect in congenital prosopagnosia. Unlike many prosopagnosic patients reported in the literature, AA's deficit is restricted to faces, and he has a high IQ with intact lower-level processing. Thus, he provides an ideal opportunity to investigate the facial information extracted by an impaired processing system relative to controls. Like other cases of congenital prosopagnosia (i.e. Schwarzer et al., in press), AA could explicitly recognise the faces of some famous people, which can limit demonstration of covert recognition. To address this, we conducted a final study involving a larger number of famous faces to evaluate AA's viewing strategy for stimuli that he could and could not recognise. This allowed us to determine whether the reprocessing effect would emerge independently of explicit remembering. Evidence of a reprocessing effect would be characterised by the following for novel faces: a longer processing time with more fixations, greater sampling of facial regions, and more time attending to the inner features and to the left side of space.

1. Experiment 1

Our aim in Experiment 1 was to replicate the face reprocessing effect in young adults and in a group of older adults. The effect was shown in younger adults by Althoff and Cohen (1999), and while there is no reason to expect a difference based on age, our replication included older adults in order to have an age-matched group for comparison with AA.

1.1. Method

1.1.1. Participants

Two groups of postgraduate students from the University of Exeter volunteered to take part in this experiment. The first group comprised 10 healthy younger adults (five males and five females). Their mean age was 22 years (SD = 1.15). The second group comprised nine healthy adults (four males and five females). Their mean age was 48 years (SD = 2.35). All participants reported normal or corrected-to-normal vision. Informed consent was obtained from all participants prior to onset of the experiment, and ethical approval for this study was granted by the Ethics Committee at the School of Psychology, University of Exeter.

1.1.2. Apparatus and materials

Forty digitalised photographs of famous people were downloaded from the Internet and were used to create two sets of 20 faces; one for younger participants and one for older participants. The faces were selected on the basis of findings from a pilot study in which 20 young adults and 20 adults were asked to rate the familiarity of faces on a scale from 1 to 5 (1 indicating "not at all familiar" and 5 indicating "highly familiar"). The final stimulus set for each age group comprised famous faces judged to be highly familiar by more than 80% of participants in the pilot study. Eleven faces of famous male personalities and nine faces of famous female personalities

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were selected for each age group. An additional set of digitalised photographs of unknown faces was downloaded from the Internet. This set of faces was matched to the two sets of famous faces as closely as possible for gender, age and perceived attractiveness.

All photographs were edited in Jasc® Paintshop Pro (Version 9.00). Each face was displayed from the neck upwards and upon a white background. Each stimulus was adjusted to 650 pixels in height and 500 pixels in width, and was displayed in the centre of a 22-inch colour monitor. Eye movements were recorded using an Eyelink system (SR Research Ltd, Canada), a video-based pupil/corneal reflex tracking device with a head movement compensation sampled at 250 Hz and spatial accuracy between half and one degree of visual angle. Eye position was monitored through a miniature infrared CCD video camera mounted on an adjustable headband, aimed at the right eye. Head movement was not restrained by a chin rest for this experiment, because the eye-tracker had an optical head-tracking camera integrated into the headband that allowed accurate tracking of the point of gaze without the necessity of fixing the head of the participant. The combined pupil/corneal reflex tracking technique used by the system is also robust to translate movements of the head relative to the camera (point of gaze being dependent upon the relative, rather than absolute, position of the pupil and corneal reflex in the camera field). Eye movements were analysed using Eyelink Data Viewer software (SR Research Ltd), which allowed periods of fixation to be identified and user-defined areas of interest to be determined within the face images (see below). In an initial calibration phase and then during all data collection, eye position on the screen was sent to a Dell host computer, which also collected information about when the stimuli were presented and what behavioural responses were produced.

1.1.3. *Eye movement parameters and dependent measures*

To analyse eye movements, the scanpath for each face was plotted. Five areas of interest were defined, as used in previous research (Walker-Smith et al., 1977): right eye (left side of space), left eye (right side of space), mouth, nose and 'other'. Any fixations falling outside of the defined feature areas were defined as 'other'. To distinguish these regions, the interest areas were drawn onto each face using a freehand marquee tool. To ensure that the average size of the interest areas did not differ between famous and novel faces, a univariate analysis of variance was carried out to compare the size of each of the four inner features. This analysis showed that the average size of each interest area did not differ between the two sets of faces.

We selected seven dependent measures based on their theoretical relevance. First, we included the standard behavioural indicator of reaction time, measuring the length of time that elapsed before a familiarity decision was made for each face. Numerous studies have indicated that familiarity judgments are typically made faster for familiar than for novel faces (e.g. Althoff and Cohen, 1999). This finding has been explained by a need to collect more data from novel faces, as the strength of the facial memories associated with these faces is naturally more limited than memories for familiar faces.

Second, two temporal fixation measures were employed to measure the amount of sampling elicited to each type of face. We measured the number of fixations per second and the average fixation duration for famous and novel faces. The number of fixations provides an index of the amount of sampling directed to an item; more sampling is associated with the need to extract more information from a face. Thus, it was hypothesized that more fixations would be elicited to novel faces. Fixation durations in scene viewing have a mean of about 300 msec (Henderson and Hollingworth, 1998), yet there are also reports of substantial variability in this value. This variability may reflect shorter fixation durations as a result of semantic constraint (Friedman, 1979; Henderson et al., 1999; Loftus and Mackworth, 1978) or prior exposure (Friedman, 1979). Indeed, it is possible this measure may be influenced by familiarity.

Two additional variables associated with the regional distribution of scanning were measured. These were the number of regions sampled out of a possible five (right eye, left eye, nose, mouth and other) and the number of consecutive fixations made within a region (i.e. runs). The number of regions sampled provides an additional measure of the level of sampling elicited to a stimulus, while taking into account the regional distribution of scanning. It has been suggested that the number of consecutive fixations within the same region reflects an attempt to resolve regional feature ambiguity in the data generated during the first fixation of the pair (Barton et al., 2006). If so, repeated scanning may be related to local feature-based processing, as opposed to the generation of the global face percept. It is likely this process may be heightened in prosopagnosia based on the hypothesis that these patients tend to rely on a feature-based scanning strategy.

Finally, two measures providing an index of the spatial distribution of scanning were taken. These were the proportion dwell time spent viewing the right hemispace and the inner features. These two measures are particularly important given we used faces as stimuli. There is considerable evidence from eye movement studies that attention is directed predominantly to the inner features during recognition (i.e. the eyes, nose and mouth), with fewer fixations made to the external features (Groner et al., 1984; Henderson et al., 2001; Luria and Strauss, 1978; Mertens et al., 1993; Walker-Smith et al., 1977). Further, Althoff and Cohen (1999) found this bias was affected by familiarity, with greater sampling of the inner features for novel compared to famous faces. In contrast, evidence from the behavioural literature suggests that the internal features of a face are more important for recognition when the face is familiar than when it is unfamiliar (Clutterbuck and Johnston, 2005; Ellis et al., 1979; Young et al., 1985). Thus, additional evidence from a scanning study that manipulates familiarity will help to resolve this ambiguity. Further, a recent study has indicated that patients with congenital prosopagnosia fixate on external facial features to a greater extent than control participants when viewing both famous and unfamiliar faces (Schwarzer et al., in press). These authors attributed this finding to the relationship between fixation behaviour and expertise (Viviani, 1990); skilled professionals tend to focus their fixations on details which are meaningful to themselves as experts, whereas

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laymen tend to search for other informative regions. In prosopagnosia, the places with high informative value are not the inner features but other external features that can also be useful for recognition. The case of AA presents a further opportunity to examine this hypothesis.

Finally, the asymmetry of face perception has a long history. A left hemifield advantage, interpreted as a consequence of a right hemispheric specialization for face processing, has been demonstrated in fMRI experiments showing predominant activation of the right fusiform gyrus by faces (Kanwisher et al., 1997; Rossion et al., 2002), in eye-tracking studies showing greater dwell time on the right side of a face (Althoff and Cohen, 1999; Butler et al., 2005; Gilbert and Bakan, 1973; Mertens et al., 1993) and patient studies showing that prosopagnosia from unilateral lesions is more likely to result from right rather than left occipito-temporal damage (Barton, 2003). Althoff and Cohen (1999) note a further advantage associated with asymmetric viewing. They claim that avoiding symmetry in scanning results in a more efficient strategy for extracting important information from the face. Whether this left hemifield advantage is apparent in congenital prosopagnosia has not yet been demonstrated.

1.1.4. *Procedure*

Participants were seated in a quiet room, approximately 60 cm from the screen. No bite bar or chin rest was used given the eyelink system had built-in head movement compensation. A calibration of eye fixation position was conducted prior to the experiment. This calibration procedure began with the presentation of a white dot in the centre of a black computer screen. The dot moved consecutively around the edge of the screen until an adequate corneal lock was achieved in each position. Once each participant had successfully completed the calibration phase, they immediately progressed to the recognition test. Because the test was administered in one continuous block, recalibration was not necessary.

Participants viewed the sequence of 40 stimuli (20 known and 20 unknown) in a random order, with an exposure time of 5 sec per face. Participants were required to make a recognition judgment for each face, pressing the right key on a joypad if the face was familiar to them and the left button if the face was unknown. They were also informed that reaction time would be recorded. Each face was presented for exactly 5 sec, whether or not a response had been provided, and the visual scanpath was recorded for the entire duration. The initial point of retinal attention was controlled by the presentation of a centrally positioned fixation dot before each stimulus appeared. The next stimulus was displayed once the participant had recommitted their attention by fixating on the dot.

1.1.5. *Statistical analyses*

Analyses were conducted on data collected from each dependent variable within the reaction time period (i.e. until participants signified recognition). The data were divided into responses for the 20 familiar and 20 unfamiliar trials for each participant. As no errors were made by any participant, no trials were removed from the analyses. However, as in previous research, response latencies that differed by two or more standard deviations from the mean were removed from all dependent measures. Using this strategy, a total of 57 trials (out of a possible 760) were removed from analysis. We then examined the effect of familiarity on each of our seven variables. The mean score for each variable was calculated for famous and novel faces for each participant, and placed into a 2 (familiarity: famous, unknown) × 2 (age: old, young) mixed factorial analysis of variance with repeated measurements on the 'familiarity' factor.

1.2. *Results*

1.2.1. *Accuracy and reaction time*

All participants correctly categorised all faces as famous and novel. Mean reaction times were 938.25 msec for famous faces and 1439.10 msec for unknown faces (S.E.s = 71.32 and 148.05), and this difference was significant: $F(1,17) = 13.041$, $p = .002$ (see Table 1). There was no influence of age on this measure, $F(1,17) = .119$, $p = .735$.

1.2.2. *Overall viewing patterns*

To obtain a general indication of viewing strategy, the mean percentage dwell times for each of the five areas of interest (left eye, right eye, mouth, nose and other) were calculated for famous and novel faces. These data were entered into a 2 (familiarity: famous, novel) × 2 (age: old, young) × 5 (region) analysis of variance, with repeated measurements on the 'familiarity' and 'region' factors. Attention largely concentrated on the four inner features, with the majority of time spent viewing the nose, as supported by a main effect of region of face $F(3,51) = 5.750$, $p = .006$[1] (see Table 2). Further, there was a significant three-way interaction between familiarity, age and region, $F(3,51) = 3.835$, $p = .022$. Post hoc comparisons revealed older participants spent less time on the mouth and more time on the nose for famous faces, $F(1,17) = 7.263$, $p = .015$, yet there was no difference in the amount of dwell time spent on these features for younger participants.

1.2.3. *Fixation measures*

A greater number of fixations were made per second to novel faces ($M = 3.61$, S.E. = .25) than to famous faces ($M = 3.32$, S.E. = .29) and this difference was significant: $F(1,17) = 8.810$, $p = .009$. Accordingly, fixation durations were significantly longer for famous faces ($M = 377.88$ msec, S.E. = 32.79) than for novel faces ($M = 316.48$ msec, S.E. = 24.69), $F(1,17) = 8.538$, $p = .010$. Neither fixation rate nor fixation duration were found to be influenced by the age of participants, $F(1,17) = .208$, $p = .654$ and $F(1,17) = 1.308$, $p = .269$.

1.2.4. *Interest area measures*

As predicted, the number of regions sampled for novel faces ($M = 2.38$, S.E. = .13) was significantly greater than for famous faces ($M = 1.78$, S.E. = .11): $F(1,17) = 33.455$, $p = .001$. Viewing patterns within each region also differed according to previous exposure. The number of runs (consecutive fixations within a region) made for novel faces ($M = 3.23$, S.E. = .33) was also significantly higher than that for famous faces ($M = 2.05$, S.E. = .19): $F(1,17) = 17.818$, $p = .001$. Neither of these two

[1] Huynh–Feldt correction used throughout.

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Table 1 – The mean (standard deviation) performance of controls (Experiment 1) and AA (Experiment 2) on measures of the reprocessing effect

	Control participants		AA	
	Famous	Novel	Famous	Novel
Reaction time (msec)	938.25 (310.86)	1439.10 (645.34)	1304.37 (444.83)	1977.61 (685.25)
Fixation rate per second	3.32 (1.28)	3.61 (1.09)	2.82 (1.23)	2.56 (.94)
Fixation duration (msec)	377.88 (142.93)	316.48 (107.63)	467.80 (185.94)	413.22 (169.25)
Region count	1.78 (.50)	2.38 (.58)	1.90 (.57)	2.56 (1.20)
Run count	2.05 (.84)	3.23 (1.42)	2.42 (.96)	3.50 (2.09)
Proportion inner (%)	68.14 (8.57)	73.38 (7.40)	66.37 (28.24)	83.90 (19.12)
Proportion left (%)	45.41 (15.81)	48.90 (11.63)	40.41 (32.30)	50.51 (31.58)

measures were influenced by age, $F(1,17) = 1.429$, $p = .248$ and $F(1,17) = .001$, $p = .987$.

1.2.5. *Dwell time measures*

A greater proportion of dwell time was spent on the inner features than 'other' regions for both famous ($M = 68.14\%$) and novel ($M = 73.38\%$) faces (S.E.s = 1.20 and 1.70), and a significantly greater proportion of dwell time was spent on the inner features for novel faces than for famous faces: $F(1,17) = 7.900$, $p = .012$. There was no effect of age, $F(1,17) = .001$, $p = .997$. Although no main effect of familiarity was found for percentage dwell time spent on the left side of space, $F(1,17) = 2.037$, $p = .172$ (see Table 1), a significant interaction between familiarity and age was found. Younger adults spent less time on the left side of space for famous people than they did for novel faces, as predicted, but this was not the case for the adult group: $F(1,17) = 23.081$, $p = .001$. In younger adults, the difference between time spent on the left side for famous faces ($M = 35.62\%$) and novel ($M = 48.58\%$) faces (S.E.s = 3.82 and 3.78) was significant: $F(1,9) = 97.271$, $p = .001$. Hence, the predicted reprocessing effect for this indicator was only found in younger participants.

1.3. *Summary of Experiment 1*

Experiment 1 aimed to replicate the reprocessing effect originally reported by Althoff and Cohen (1999) with famous faces. The viewing of novel faces was characterised by slower reaction times, more fixations per second, shorter duration of fixations, more attention to the inner features, more regions sampled and more runs (i.e. consecutive fixations) made within regions for novel faces. However, the predicted effect was only found in younger participants for the proportion dwell time spent on the left side of space.

2. Experiment 2

The aim of this study was to explore whether the reprocessing effect would emerge in a congenital prosopagnosic (AA). The same design and dependent measures used in Experiment 1 were repeated with AA. Investigation of the reprocessing effect with AA was conducted in two stages: the first involved comparison of AA's viewing of famous faces to his viewing of novel faces, regardless of response accuracy; and the second, a comparison of AA's viewing patterns to those of controls for each type of face.

2.1. *Method*

2.1.1. *Participant*

AA is a 57-year-old right-handed male who had been educated to degree level, and is currently employed as a teacher of physics. He reported a history of face recognition problems since early childhood, with a specific memory of attending a birthday party at around six years of age where he could not recognise any of his peers. AA currently reports problems recognising his grown-up children from photographs taken in their childhood, and when meeting them at the train station. AA has no history of neurological or psychiatric illness that may have contributed to his difficulty with faces, and no abnormalities were detected on structural MRI scanning.

Results of neuropsychological testing show AA to be a highly intelligent gentleman. Despite intact lower-level

Table 2 – Mean percentage dwell times (standard deviation) spent on each feature by control participants (Experiment 1) and AA (Experiment 2)

	Control participants		AA	
	Famous	Novel	Famous	Novel
Left eye	16.48 (18.29)	14.57 (9.30)	24.93 (25.91)	11.63 (14.22)
Right eye	12.56 (11.16)	19.32 (14.24)	8.44 (11.68)	4.29 (7.84)
Mouth	10.23 (9.50)	13.54 (11.09)	5.22 (9.09)	4.72 (8.08)
Nose	32.07 (17.57)	29.64 (15.65)	38.95 (28.42)	50.41 (33.49)
Other	28.66 (9.50)	22.93 (6.32)	22.47 (25.81)	28.95 (25.16)

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Table 3 – AA's neuropsychological profile

Function	Test	Score
General intellectual function (WAIS III)	Full scale IQ	142
	Verbal IQ	135
	Performance IQ	140
Memory (WMS III)	General memory	120
	Visual immediate memory	115
	Visual delayed memory	118
Object processing (BORB)	Object decision	123/128
	Foreshortened match	25/25
	Minimal feature match	25/25
	Line orientation	25/30
	Position of gap	35/40
Face processing		
Matching	Benton Face Recognition Test	39[a]
Recognition	Hodges and Ward Famous Faces Test	Faces: 20/32[a]; Names: 32/32
Naming	Matched Face and Objects Test	Faces: 16/62[a]; Objects: 44/62
Memory	Warrington Recognition Memory	Faces: 32/50[a]; Words: 45/50
	Doors and People (scaled scores)	People: 8[a]; Doors: 13; Shapes: 14; Names: 15
	Cambridge Face Memory Test	*Upright*. Intro: 16[a]; Novel images: 15[a]; Novel with noise: 9[a]; Overall: 40[a]
		Inverted. Intro: 14; Novel images: 16; Novel with noise: 8; Overall: 38

a Indicates impaired performance.

vision and unimpaired object recognition, evidenced in his performance on various subtests of the BORB (see Table 3), AA's difficulties in recognising faces were evident in tests of face processing. AA performed at chance on tests requiring him to learn and recognise pictures of unfamiliar faces (i.e. the Warrington Recognition Memory Test; Warrington, 1984) and the Doors and People Test (Baddeley et al., 1994). He performed just within the normal range on the Benton Test of Face Matching (Benton et al., 1983), yet his responses were slow. Reliance on the Warrington and Benton tests for diagnostic purposes is inadequate as they tend to produce inconsistent results with this population; some individuals with developmental or congenital prosopagnosia are impaired on these tests (e.g. Ariel and Sadeh, 1996; de Gelder and Rouw, 2000), and others perform within the normal range despite clear impairment on tests of familiar face recognition (e.g. Duchaine, 2000; Nunn et al., 2001). Furthermore, the validity of these standardized tests has been criticised because the photographs in these tests contain non-facial cues such as hairstyle and clothing (Duchaine and Weidenfeld, 2003; Kress and Daum, 2003). Indeed, AA's performance on the Cambridge Face Memory Test (Duchaine and Nakayama, 2006), developed in response to criticisms of the standardized clinical tests, showed impaired recognition for upright faces but better recognition of inverted faces (i.e. the face inversion effect). This profile is consistent with the sample of people with developmental prosopagnosia reported on this test (Duchaine and Nakayama, 2006). AA was also poor in recognising pictures of famous faces. In the Hodges and Ward (1989) Famous Faces Test, AA correctly chose the famous person from a choice of four faces (one famous, three unknown) in only 20 out of 32 trials. This was impaired compared to the age-related mean score of 29 in healthy participants. Importantly, in a name version of this task, his recognition of the names of the same target famous people was perfect, suggesting good recognition of people in another modality. As AA's performance on the WMS III shows he does not have a generalized deficit of non-verbal memory, it appears his impairment is isolated to the processing of faces. Further neuropsychological history on this case is presented in the study reported by Tree et al. (submitted for publication).

The above evidence indicates that AA fulfils the criteria of Jones and Tranel (2001) for congenital prosopagnosia: he presents with a lifelong impairment in face processing, in the absence of any neurological illness or injury, and has intact visual and intellectual functions. The impairment in AA appears to be closer to the "associative" rather than "apperceptive" subtype of prosopagnosia, given his intact performance on tests of lower-level vision and face-matching tasks.

2.1.2. *Materials and procedure*

The same stimuli and procedure employed in Experiment 1 were used in this study. On completion of the study, AA was presented with all the faces a second time in a random order. His task was to judge faces as famous or novel, and to explicitly identify (by name or provision of uniquely identifying semantic information) those faces he categorised as famous. In addition, he was asked to provide a confidence rating for each of his responses on a scale ranging from 1 (not at all confident) to 5 (very confident).

2.1.3. *Statistical analyses*

All trials were included in data analysis and separated for famous and novel faces. Thus, incorrect responses were not removed from the analyses for AA. Trials that differed by more than two standard deviations from the mean score on

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reaction time were removed, and AA's performance on each dependent measure was compared across famous and novel faces using univariate analyses of variance. To examine AA's performance in relation to that of controls, data were converted into z scores using the mean and standard deviation for the control participants. Experiment 1 showed that our older and younger controls performed similarly on the majority of eye-tracking measures, except for the proportion dwell time spent on the left side of space. With the exception of this latter measure, control data were merged for comparison with AA in order to increase the power of our analyses. The cutoff for normal performance was set at a z score of 1.96, corresponding to the top and bottom 2.5% of the normal distribution.

2.2. Results

2.2.1. Accuracy and reaction time

When performing the recognition test, AA correctly judged all the 20 novel faces to be unfamiliar, and correctly judged 17 of the 20 famous faces to be familiar (85%). However, his mean confidence rating was low particularly in response to famous faces (2.6 out of 5, range 1.0–3.5) and slightly higher for novel faces (3.2 out of 5, range 2.0–5). Further, when asked to explicitly identify the famous people after the test, AA only named or provided uniquely identifying semantic information for 10 of the 20 famous people (50%), despite being highly familiar with all the targets in response to name cues. Thus, his high accuracy rate on the forced-choice behavioural measure of accuracy suggests some degree of implicit recognition in this patient, beyond the level of conscious awareness.

AA's response latencies were faster for famous faces than they were for novel faces, with a mean reaction time of 1304.37 msec for famous faces and 1977.61 msec for novel faces, and this difference was significant: $F(1,35) = 12.702$, $p = .001$. AA's reaction times did not differ from those of controls for either famous or novel faces (see Table 1).

2.2.2. Overall viewing patterns

A two (familiarity: famous, novel) by five (region: right eye, left eye, mouth, nose, other) mixed design analysis of variance did not reveal a difference in the viewing time spent on each region according to the familiarity of the face, $F(4,140) = 1.526$, $p = .198$ (see Table 2). However, a main effect of region indicated that AA did spend more time viewing certain regions irrespective of the type of face, $F(4,140) = 17.534$, $p = .001$. Specifically, a post hoc contrast indicated he spent significantly more time viewing the nose than any other region, $F(1,35) = 23.451$, $p = .001$. The proportion of dwell time spent on each feature did not differ from that of age-matched controls.

2.2.3. Fixation measures

The mean number of fixations made per second by AA was 2.82 for famous faces and 2.56 for novel faces. This did not differ between the two types of face, $F(1,35) = .542$, $p = .467$, and was within the normal range displayed by age-matched control participants (see Table 2). AA's mean fixation duration was 467.80 msec for famous faces and 413.22 msec for novel faces. This difference was not significant: $F(1,35) = .695$, $p = .410$. These values were within the normal range found in our control participants.

2.2.4. Interest area measures

AA sampled a mean of 1.90 regions for famous faces and 2.56 regions for novel faces. This difference was significant, $F(1,35) = 4.673$, $p = .038$. AA made an average of 2.42 runs (consecutive fixations) within each region for famous faces and 3.50 for novel faces. Significantly more runs were made for novel than famous faces, $F(1,35) = 4.133$, $p = .050$. AA's performance on both of these measures fell within the control range.

2.2.5. Dwell time measures

AA spent 66.37% of dwell time on the inner features of famous faces and 83.90% of dwell time on the inner features of novel faces. Thus, as predicted, he spent more dwell time on inner features for novel faces than for famous faces and this difference was significant, $F(1,35) = 4.833$, $p = .035$. Further, AA spent 40.41% dwell time on the left side of space for famous faces and 50.51% for novel faces. This difference was not significant, $F(1,35) = .924$, $p = .343$. AA's performance on both of these measures was in the control range.

2.3. Summary of Experiment 2

In this study we used eye-movement measures to assess the relationship between face perception and recognition in a person with congenital prosopagnosia, AA. Our first aim was to investigate whether a reprocessing effect could be observed in AA's pattern of eye movements for famous faces, irrespective of his recognition accuracy. Second, we compared AA's performance to that of a group of healthy control participants. A difference in the processing of famous and unfamiliar faces was found on four dependent measures: reaction time, number of regions sampled, number of runs (or consecutive fixations within the same region), and the proportion dwell time spent on the inner features. Yet, the effect was not entirely consistent with that displayed by controls: for AA there was no difference between famous and novel faces on the two fixation-based measures, fixation count and fixation duration.

AA's scanpath strategy in the context of his recognition performance requires further examination. The above analyses did not take recognition accuracy into account. We know that AA was able to provide uniquely identifying information for half the faces in the stimulus set, and thus it might be argued that the eye movement-based memory effect was driven largely by responses to faces he explicitly recognised. Accordingly, this does not provide evidence of covert recognition using eye-tracking indicators. More convincing evidence would be provided if the eye movement-based memory effect could be demonstrated separately for faces he could and could not recognise explicitly. The stimulus set in this experiment was not sufficiently large to address this question, and hence a third experiment was conducted in which a larger set of famous and novel stimuli were used.

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3. Experiment 3

Having demonstrated at least some evidence of an eye movement-based memory effect in AA, the aim of the present study was to investigate the same effect for faces he could not recognise explicitly. Explicit recognition was defined as provision of the correct name of the target personality or of accurate semantic information. The same procedure used in Experiments 1 and 2 was repeated here with a larger set of stimuli. Evidence of a reprocessing effect for famous faces AA could not recognise would provide evidence of residual covert face processing abilities.

3.1. Method

3.1.1. Materials and procedure

The same procedure used in Experiments 1 and 2 was repeated in Experiment 3. However, the number of stimuli was increased from 40 to 60, with 30 additional famous and 30 additional novel faces presented for recognition. The famous faces were identified as highly familiar by a group of 20 age-matched participants. As in Experiment 2, AA was asked to view the set of faces a second time, once the eye-tracking data had been recorded. In this second viewing session, he was again asked to classify the faces as novel or famous, and to explicitly identify those faces that he recognised. AA was also asked to provide confidence ratings on a scale ranging from 1 (not at all confident) to 5 (very confident) for each familiarity and identification judgment.

3.1.2. Statistical analyses

Data collected in Experiments 2 and 3 were pooled, resulting in 50 novel and 50 famous faces for analysis. Responses for each dependent measure were separated for novel and famous faces, and further subdivided into those famous faces that were explicitly recognised and those that were not. Those trials that differed by more than two standard deviations from the mean on reaction time were excluded. On this basis, one famous face that was explicitly recognised, one that was not explicitly recognised and one novel face were excluded. Univariate analyses of variance and planned comparisons were then carried out for each dependent measure to make two comparisons between (1) explicitly recognised famous faces and novel faces, and (2) non-recognised famous faces and novel faces.

3.2. Results

3.2.1. Accuracy and reaction time

AA correctly categorised 88 out of the 100 faces as either familiar or novel. He incorrectly categorised eight out of 50 famous faces as novel and four novel faces as famous. Again, mean confidence levels were low for famous and novel faces (2.3 and 3.4 out of 5, respectively). Explicit identification of the famous faces after the test was low, as AA could only name or provide accurate semantic information for 22 of the 50 faces (44%), despite being highly familiar with all of the famous people when informed of their identity by name.

Differences in reaction time were found between novel ($M = 1900.00$ msec) and explicitly recognised famous faces ($M = 1282.52$ msec) and the difference was significant, $F(1,94) = 12.084$, $p = .001$ (see Table 4). There was also a difference in response latencies for famous faces that AA did not recognise ($M = 1563.59$ msec) and novel faces, $F(1,94) = 4.247$, $p = .042$ (see Fig. 1).

3.2.2. Overall viewing patterns

In Experiment 3, no difference was found in AA's pattern of feature exploration according to the type of face he was viewing, $F(8,376) = .485$, $p = .867$. As in Experiment 2, a main effect of region ($F(4,376) = 53.875$, $p = .001$) and post hoc contrasts revealed he spent more time studying the nose than any other feature, $F(1,94) = 98.975$, $p = .001$.

3.2.3. Fixation measures

No difference in fixation rate was found between either recognised or non-recognised famous faces in comparison to novel faces, $F(2,94) = .216$, $p = .806$; nor was there a difference in fixation duration, $F(2,94) = .279$, $p = .757$.

3.2.4. Interest area measures

Differences in the number of regions sampled were found between both sets of famous faces when they were compared with novel faces. Fewer regions were sampled for recognised famous faces ($M = 1.86$) than for novel faces ($M = 2.43$), $F(1,94) = 6.681$, $p = .011$; and for famous faces that were not recognised ($M = 1.96$) compared to novel faces, $F(1,94) = 5.253$, $p = .024$ (see Fig. 2). Fewer runs (i.e. consecutive fixations) were made for recognised famous faces ($M = 2.33$) than for novel faces ($M = 3.29$), $F(1,94) = 5.714$, $p = .019$; and for famous faces that were not recognised ($M = 2.56$) in comparison to novel faces, $F(1,94) = 3.977$, $p = .049$ (see Fig. 3).

Table 4 – Performance of AA in Experiment 3 on measures of the reprocessing effect

	Famous faces		Novel faces
	Recognised	Not recognised	
Reaction time (msec)	1282.52 (350.52)	1563.59 (754.35)	1900.00 (740.87)
Fixation rate per second	3.58 (1.19)	3.36 (1.15)	3.44 (1.15)
Fixation duration (msec)	322.28 (147.71)	331.19 (151.83)	323.57 (143.03)
Region count	1.86 (.48)	1.96 (.85)	2.43 (.96)
Run count	2.33 (.86)	2.56 (1.50)	3.29 (1.74)
Proportion inner (%)	70.08 (22.62)	71.52 (25.61)	83.34 (16.31)
Proportion left (%)	50.87 (32.18)	50.70 (30.94)	50.30 (28.43)

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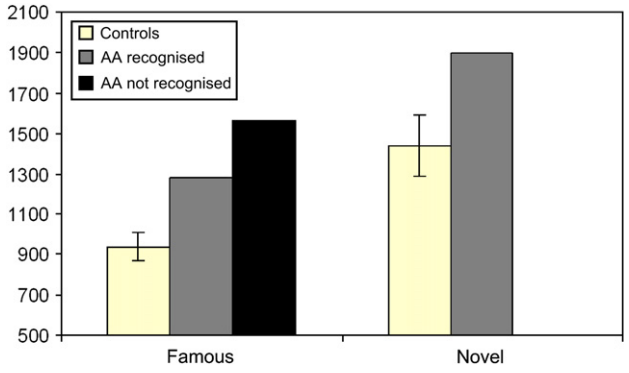

Fig. 1 – AA's mean reaction time (msec) for each type of face in comparison to control participants.

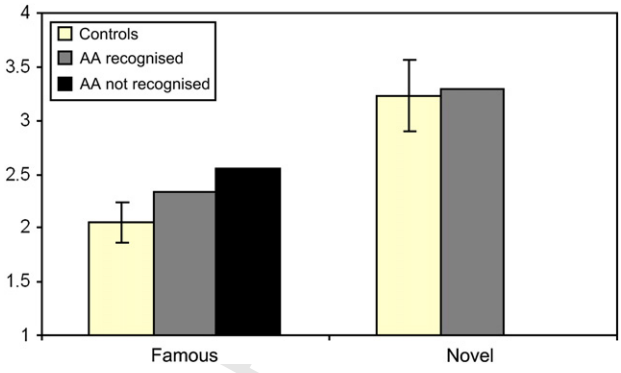

Fig. 3 –

3.2.5. *Dwell time measures*

A difference in the proportion dwell time spent on the inner features was found between recognised famous faces ($M = 70.08\%$) and novel faces ($M = 83.34\%$), $F(1,94) = 6.067$, $p = .016$; and between non-recognised famous faces ($M = 71.52\%$) and novel faces, $F(1,94) = 3.977$, $p = .049$ (see Fig. 4). However, no difference was found in the proportion dwell time spent on the left side of space between either recognised or non-recognised famous faces compared to novel faces, $F(2,94) = .003$, $p = .997$.

3.3. *Summary of Experiment 3*

In Experiment 3 we investigated covert processing in a case of congenital prosopagnosia by comparing eye movement performance for explicitly recognised famous faces and for famous faces AA could not explicitly recognise relative to that for novel faces. Differences were observed between viewing patterns for recognised famous faces and novel faces on four of the seven dependent measures: reaction time, region count, run count and proportion dwell time spent on the inner features. An eye movement-based memory effect was found on the same measures for famous faces that AA could not recognise explicitly. This finding suggests an eye movement-based memory effect can be found for faces that cannot be explicitly recognised in congenital prosopagnosia.

4. General discussion

The aims of this study were (a) to replicate the eye movement-based memory effect in healthy control participants and (b) to investigate whether this effect could be used to index covert processing in a case of congenital prosopagnosia. In healthy control participants we found a difference in the viewing of novel compared to famous faces, characterised by fewer fixations and reduced sampling of facial features in familiar stimuli. Interestingly, the predicted finding that more time would be spent on the left side of space for the viewing of novel faces was only found in our younger adult controls. In Experiment 2, some evidence of reduced sampling was also found in AA, irrespective of his recognition accuracy. While this suggested that the visual scanpath could be used to discriminate novel from famous faces in congenital prosopagnosia, it was not clear whether the demonstrated effect was based on overt or covert recognition of famous faces. This was investigated in Experiment 3 where famous faces were divided into those that were explicitly recognised and those that were not. Again, a reprocessing effect was found for famous faces that AA could explicitly identify on some measures, and the same indicators were found to contribute to the effect for those famous faces that AA could not explicitly recognise.

Consistent with two previous studies that examined the influence of prior exposure on scanning strategy (Althoff and Cohen, 1999; Barton et al., 2006), the key finding in our

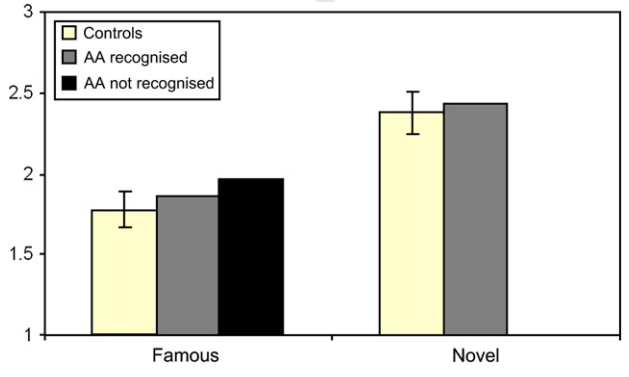

Fig. 2 –

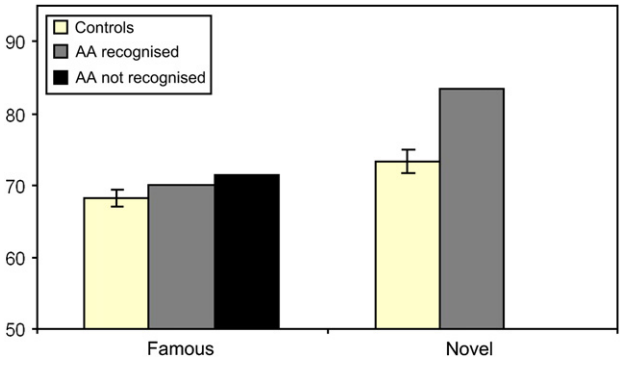

Fig. 4 –

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control participants was a reduction in the sampling of famous faces. Indeed, the viewing of familiar stimuli was characterised by shorter reaction times, fewer fixations and the sampling of fewer regions. While previous studies used a combination of these and other measures to characterise this reduction in sampling, a similar interpretation can be applied in each case. That is, information gathering for novel faces is less effective, reflected in a need to accumulate more data resulting in an increased number of fixations and longer scanning durations to reach a decision. As the strength of the internal representations of famous faces is greater, a familiarity decision can be made more rapidly, with less data required to reach the decision threshold. Further, the number of consecutive fixations within the same region was also found to differ between famous and novel faces. Barton et al. (2006) found that more regionally repetitive pairs were made for morphed (ambiguous) famous faces compared to novel faces, and suggested that continued sampling of the same region reflects an attempt to resolve regional feature ambiguity in the data generated during the first fixation of the pair. This explanation is also consistent with our findings, as further hypothesis testing would naturally occur for novel faces, whereas confirmatory evidence is likely to be received within the first fixation to a region in famous faces. However, Barton et al. did not find a similar difference for the number of runs made for non-morphed famous faces and novel faces. It is possible this discrepancy may be explained by the definition of the regions of interest: Barton et al. divided their stimuli into eight regions of interest (right and left eye, nose, mouth, chin, right and left cheek, brow) whereas we used five (right and left eye, mouth, nose and other). These differences in classification may have influenced the number of regionally repetitive pairs found in the two studies.

Findings from our control participants concerning the regional distribution of scanning speak to inconsistencies in the current literature on face processing. First, a greater proportion of dwell time was spent on the inner features for novel faces than for famous faces. This is in line with the scanning study conducted by Althoff and Cohen (1999), but in opposition to behavioural findings that suggest the inner features are more important for familiar face recognition (e.g. Clutterbuck and Johnston, 2005; Ellis et al., 1979; Young et al., 1985). An alternative explanation for this discrepancy concerns the temporal order of fixation distribution, rather than the relative importance of the internal and external features for recognition. It is likely that when a face is presented for recognition, scanning begins with the inner features for both familiar and novel stimuli. As these data are processed more rapidly for familiar faces, confirmatory evidence for identification may then be sought from the less informative external features. However, as no strong representations are available for the processing of novel faces, data extraction from the internal features is slower as hypothesis testing continues. Since an identity threshold is not reached at an early stage of scanning for these faces, the majority of scanning time is dedicated to processing the critical information within the inner features.

Further, we found the proportion dwell time spent on the left side of space to be in the predicted direction only for our younger adult participants. While evidence of right hemisphere dominance in face processing has a long history in the literature, other factors have been found to influence hemispheric processing of faces, such as gender (e.g. Smith, 2000). Our findings suggest that the right hemisphere dominance may also be influenced by age. Indeed, the original report of a greater bias towards the left side of space for novel faces only monitored viewing in younger adult participants (Althoff and Cohen, 1999). However, it should be noted that the two sets of participants in our study viewed a different set of faces, and the possibility that this finding was a consequence of the physical properties of the stimuli cannot be ruled out.

AA and control viewing strategies for famous and novel faces revealed some inconsistencies in performance. We found no evidence of a reprocessing effect on the two fixation-based measures for AA in either experiment. It may be that the fixation-based measures are not particularly reliable indicators of the effect for patients with impaired recognition, as these individuals may be more vigilant in their scanning strategy given awareness of their impairment. Further, the finding that proportion dwell time spent on the inner features differed between famous and novel faces in AA, and that this value did not differ from that of control participants, is not compatible with the recent report that patients with congenital prosopagnosia tend to focus on the external features to a greater extent than healthy participants (Schwarzer et al., in press). Finally, AA did not show the predicted left-sided processing bias for either novel or famous faces. This finding speaks to a recent study that suggests the right hemisphere dominance in face processing is not pre-specified, but develops in response to early visual experience in face processing (Legrand et al., 2003). Thus, in congenital prosopagnosia where impaired face processing is present from birth this right hemisphere dominance may fail to develop, and hence explain why we did not find the bias in AA.

Importantly, our findings make two further important contributions to the literature on congenital prosopagnosia. First, AA appears to represent a case of associative congenital prosopagnosia. Support for such a distinction between associative and apperceptive prosopagnosia in the literature is weak, as the majority of the congenital cases are believed to have deficits at the level of structural encoding. Further, the pattern of deficits found in these patients is varied, implying that congenital prosopagnosia is likely caused by impairments to different mechanisms in different individuals. However, in larger samples of patients it may be useful to partition the disorder, and one possibility is to use the perceptual/mnemonic distinction classically used in acquired prosopagnosia. Currently, the only congenital prosopagnosics that are reported to suffer from the associative impairment are Dr S (Temple, 1992), BC (Duchaine, 2000), and TA (Jones and Tranel, 2001); all of which show normal or near-normal performance on the Benton Test of Face Recognition and object perception as well as a reasonable capacity to judge the sex, expression and age of faces. AA shows the same pattern in performance and thus strengthens the case for an associative and apperceptive distinction in congenital prosopagnosia. Further, the evidence reviewed here suggests that eye movement monitoring may provide an effective means of discriminating between different subtypes of congenital prosopagnosia.

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Second, two previous studies have failed to find evidence of covert recognition in congenital prosopagnosia using behavioural indicators (Bentin et al., 1999; de Haan and Campbell, 1991). These findings are consistent with the view that covert recognition in acquired prosopagnosia is dependent upon subthreshold activation of face representations acquired prior to brain damage. Arguably, as people with congenital prosopagnosia have never had normal face processing abilities, it seems plausible that they would not be able to covertly activate face representations (Barton et al., 2001). Contrary to this suggestion, evidence of covert recognition has recently been shown in a five-year-old boy with congenital prosopagnosia using SCR (Jones and Tranel, 2001). Given this, an alternative explanation may be that covert recognition can only be found using autonomic but not behavioural measures in congenital prosopagnosia, a prediction that is compatible with dual-route models of face processing (e.g. Ellis and Young, 1990).

However, the evidence reported here refutes both these explanations. Our findings suggest that, at least in some cases of congenital prosopagnosia, normal face representations may be accessed covertly. Indeed, the evidence presented here suggests that AA has relatively intact internal representations of faces, at least to the extent that he can activate some pre-existing stored representation for famous faces, even when he cannot explicitly recognise those faces. This is consistent with the neurological findings in cases of congenital prosopagnosia. Specifically, there is evidence of normal activation of the fusiform face area (FFA) in fMRI studies of congenital prosopagnosia (Avidan et al., 2005; Hasson et al., 2003; although see Hadjikhani and de Gelder, 2002); a region in the occipito-temporal cortex that responds more to faces than to most other stimulus categories (Kanwisher et al., 1997; McCarthy et al., 1997). However, in an fMRI study of four individuals with congenital prosopagnosia, Avidan et al. (2005) reported a critical difference in BOLD activity for faces in prefrontal cortex, suggesting these individuals might be taxing working memory more than normal subjects when required to process faces. Thus, in congenital prosopagnosia, an apparently normal FFA may nevertheless show inefficient interactions with working memory and attention. This may be the case with AA; he may have the ability to store relatively normal and stable internal representations, yet the connections with other parts of the perceptual and semantic systems are weakened. These weakened connections may still permit residual recognition, as indexed by indicators of covert recognition.

Our study is the first to provide evidence of covert recognition in congenital prosopagnosia using behavioural indicators. Having shown this, we propose that it is in fact the *nature of the impairment* that is predictive of the ability to display covert recognition in this condition, rather than the *indicator* (i.e. behavioural or autonomic). Perceptual tests of face recognition revealed impairments in YT and AB, and these patients also reported associated visual impairments. However, both TA and AA are cases presenting with an associative impairment demonstrated by relatively intact face and object perception. Accordingly, one might predict that patients with associative congenital prosopagnosia should demonstrate covert recognition on both behavioural and autonomic measures. From AA we have evidence of covert recognition using a behavioural measure and from TA we have such evidence from use of an autonomic measure. In future it will be important to show evidence of covert recognition using both measures in the same case. What is not clear from this research is whether the apperceptive/associative distinction is of the same nature as that reported in acquired prosopagnosia. Indeed, many authors have noted that congenital prosopagnosia is not a homogeneous disorder, and thus it is very unlikely such a fine grained distinction occurs in all cases. It is possible that the presentation of perceptual and semantic impairment may vary in different cases, and that these differences may impact on their potential to demonstrate covert recognition. Hence, not only must we examine the presence or absence of covert recognition, but also this must be done in the context of the form the prosopagnosia takes.

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