

## Normal gaze discrimination and adaptation in seven prosopagnosics

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### ABSTRACT

Sensitive gaze perception is critical for social interactions. Neuroimaging and neurophysiological results and the unique demands of gaze processing have led to suggestions that gaze is processed by different mechanisms than other aspects of faces. Neuropsychological data however provides little support for this possibility. We administered gaze discrimination tasks to six developmental prosopagnosics and one acquired prosopagnosic who exhibit identity perception deficits. First we examined whether the prosopagnosic participants could discriminate between straight and averted gaze normally. The performance of the control and prosopagnosic groups was very similar, and all of the prosopagnosics scored in the normal range. To assess whether the prosopagnosics represented gaze information like the controls, participants were tested on the discrimination task following adaptation to leftward and rightward gaze. The control and prosopagnosic groups both showed strong adaptation in the expected direction, and each prosopagnosic showed normal post-adaptation performance. These results indicate that gaze discrimination and representation is normal in these prosopagnosics. Their dissociation between impaired identity perception and normal gaze perception provides support for models of face processing suggesting that these aspects of face processing involve separate mechanisms.

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Gaze direction provides information critical to inferences about the mental state of the observed individual (Baron-Cohen, 1995). Although a wide range of species exhibit sensitivity to head direction (Burghardt, 1990; Perrett et al., 1985), humans, unlike other primates, have evolved an eye with a sharp contrast between the sclera and the iris, presumably to make gaze direction computations more accurate (Kobayashi and Kohshima, 1997). Psychophysical studies have demonstrated that humans are very sensitive to this information (Gibson & Pick, 1963), with Anstis, Mayhew, and Morley (1969) estimating that humans are sensitive to iris displacements of only 0.18 mm from the frontal view at 122 cm from the observer.

The unique demands of gaze perception as well as neurophysiological and neuroimaging studies raise the possibility that gaze perception relies on separate mechanisms than other aspects of face processing. Single cell studies in macaques have found neurons that are sensitive to head and gaze direction and others that are sensitive to facial identity (Perrett et al., 1985; Rolls & Tovee, 1995). Similarly, fMRI studies in humans suggest that the facial identity representation is especially dependent on posterior fusiform gyrus

(Hoffman & Haxby, 2000; Yovel & Kanwisher, 2005) whereas gaze relies on regions in the superior temporal sulcus (STS) (Hoffman & Haxby, 2000; Pelphrey, Viola, & McCarthy, 2004). These findings and others examining expression processing (Andrews & Ewbank, 2004; Winston, Henson, Fine-Goulden, & Dolan, 2004) led Haxby, Hoffman, and Gobbini (2000) to propose that invariant aspects of faces such as identity and gender are processed in fusiform gyrus whereas changeable aspects such as gaze and expressions are processed in the STS.

### 1. Adaptation to gaze direction

Recent behavioral studies using adaptation to leftward or rightward gaze indicate that different gaze directions may be coded by separate neural populations (Jenkins, Beaver, & Calder, 2006). During the 5-min adaptation period, participants viewed a series of frontal shots of faces displaying gaze 25° to the left or right of center. Participants were then asked to make gaze direction judgments from faces with straight gaze or gaze averted 5° or 10° to the right or left. Participants adapted to leftward gaze were much more likely to report that gaze 5° and 10° to the left was straight than they were in the pre-adaptation phase. Complementary results were found following adaptation to rightward gaze. To determine whether the adaptation effects were driven by low-level adaptation, the size and

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head orientation of the test and adapting stimuli were varied, but adaptation effects in these conditions were very similar to those found in the original experiment. Gaze adaptation does not appear to have a general effect on spatial representations, because adaptation to averted gaze had no effect on a task requiring judgment of the position of a vertical bar relative to a horizontal bar with which it intersected.

The neural basis of these effects was examined in an fMRI study comparing neural responses to different gaze directions after no adaptation, rightward adaptation, and leftward adaptation (Calder et al., 2007). Two areas showed a differential response following adaptation— anterior STS and the inferior parietal cortex. In these areas, adaptation to leftward gaze led to a weaker response to left gaze stimuli relative to right gaze stimuli, and corresponding effects were found following adaptation to rightward gaze. A study measuring evoked response potentials using the same behavioural methods found data consistent with the effects in the fMRI study (Schweinberger, Kloth, & Jenkins, 2007). The N170 is a face-selective component believed to be produced by occipito-temporal regions, and it did not respond differently following adaptation to left or right gaze. Unlike the N170, later ERPs (250–350 post-stimulus onset) were modulated weakly by the direction of gaze during the adaptation period, an effect that may reflect the involvement of the more anterior regions identified in the fMRI study (Calder et al., 2007).

## 2. Gaze discrimination in neuropsychological subjects

Although considerable evidence indicates that the perception of facial identity and gaze are processed separately, the few neuropsychological reports that have examined identity and gaze perception have not demonstrated a dissociation between them. Three prosopagnosics have been tested with a task requiring subjects to decide which of two sequentially presented faces displayed direct gaze. Head position could be straight or 20° to the right or left, and the eyes could be directed at the viewer or be 5°, 10°, or 20° to the viewer's right or left. R.B., an acquired prosopagnosic with problems with both identity and expression, scored out of the normal range and was significantly worse than controls with right hemisphere damage without prosopagnosia (Perrett et al., 1988). The same task was also used with two other prosopagnosics (Campbell, Heywood, Cowey, Regard, & Landis, 1990), an acquired prosopagnosic with right posterior damage (K.D.) and a developmental prosopagnosic featured in other papers (A.B.) (Campbell & de Haan, 1992; McConachie, 1976). Both K.D. and A.B. showed deficits on a number of face processing tasks involving identity, expression, age, and gender. K.D.'s accuracy with upright faces on the gaze task was out of the normal range while A.B. was at chance. A.B.'s decisions appeared to be driven solely by head position.

Selective lesions to STS are rare, but one case with a circumscribed lesion to the right superior temporal gyrus (STG), which forms the upper bank of the STS, was recently reported (Akiyama et al., 2006a). In face-to-face interactions, M.J.'s gaze had a tendency to drift to her left. She was tested with three gaze discrimination tasks, and as predicted by the neuroimaging results discussed above, she scored poorly on all three tasks. Interestingly, she showed a strong bias to perceive gaze to be directed to her right. A follow-up experiment used a spatial cueing paradigm to examine the specificity of her impairment (Akiyama et al., 2006b). Controls and M.J. detected peripheral targets more quickly when arrows were predictive of the target location than when they were non-predictive. However, when gaze was used rather than arrows only controls showed a congruency advantage; M.J.'s performance was not modulated by the direction of gaze. Given the location of her lesion, M.J. may have intact perception of facial identity but no data relevant to this issue have been published.

## 3. Current study: gaze discrimination and adaptation in prosopagnosia

To examine whether facial identity perception and gaze perception are dissociable as predicted by a leading model of face processing (Haxby et al., 2000), we tested a group of prosopagnosics, six developmental and one acquired, with the discrimination and adaptation tasks discussed above (Jenkins et al., 2006; Calder et al., 2007). The baseline discrimination allowed us to assess whether the prosopagnosics showed impairments with a gaze perception task. It is possible, however, that individuals with impaired gaze perception could appear normal on the gaze discrimination task using alternative strategies rather than the apparently effortless process that individuals with normal gaze perception use. To assess whether the prosopagnosics represent gaze information in the same manner as controls, we also tested their gaze perception following adaptation to leftward or rightward gaze.

## 4. Methods

### 4.1. Participants

The seven prosopagnosic participants contacted the Harvard/UCL Prosopagnosia Research Center (<http://www.faceblind.org>), because they frequently experience problems with face recognition in everyday life. We will refer to these individuals with their gender (M or F) and their age at testing. Six prosopagnosic participants have no history of brain damage, and so appear to be developmental prosopagnosics. In 2000, F54 experienced the sudden onset of a severe occipital headache associated with nausea and vomiting. A CT scan showed a subarachnoid hemorrhage due to a ruptured aneurysm in her posterior right hemisphere, and she underwent surgery to clip the aneurysm the following day. F54 reports that her face recognition was normal prior to these events, but she has had great difficulties with face recognition since then. She has recovered well otherwise.

All the prosopagnosics had normal or corrected-to-normal vision and performed normally on a visual acuity test and the tests of low-level vision from the Birmingham Object Recognition Battery (see Table 1; Riddoch & Humphreys, 1993). All have attended university.

Control groups for tests discussed below varied because the tests were developed separately so each group will be described along with the test. These studies were approved by the ethics committee at University College London, and all participants provided their informed consent before inclusion in the study.

### 4.2. Face recognition performance

To establish that the prosopagnosic participants have face recognition difficulties, we tested them with two tests of face memory. Because the gaze task we will use is perceptual, we will then present results from two tests of face perception to demonstrate that their problems with faces are perceptual and not restricted to memory.

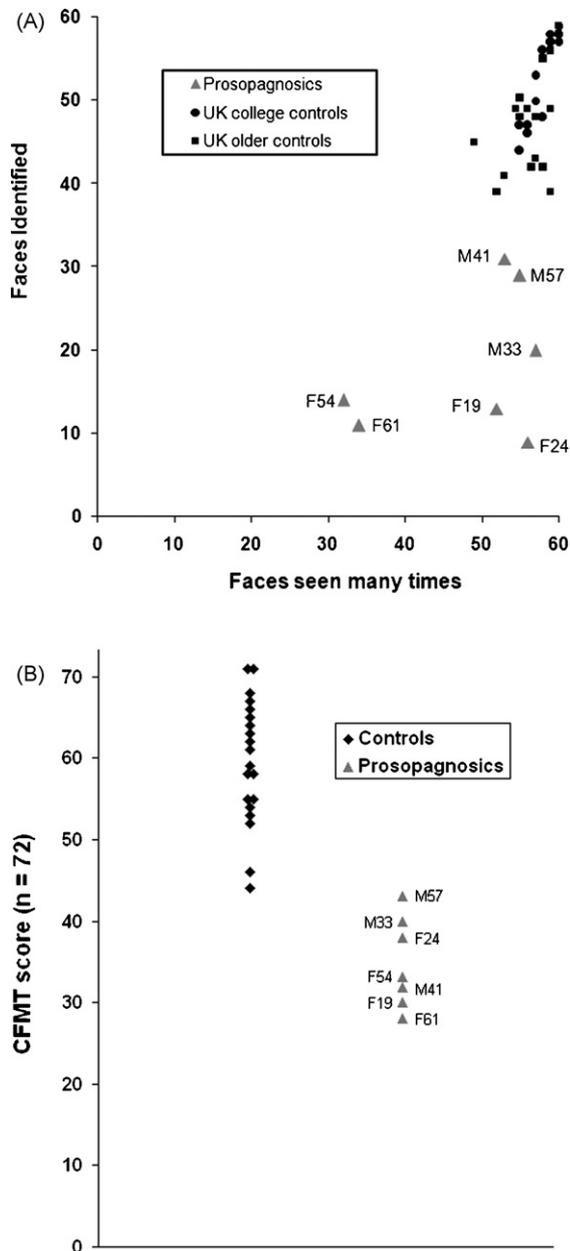
#### 4.2.1. Famous face recognition

Two different famous face tests were used: a version for the American participant (Yovel & Duchaine, 2006) and a version for British participants. In both versions, 60 images were cropped so that little hair or clothing was visible. Faces in the American version were presented for 5 s each and those in the British version were presented for 3 s each. Participants were asked to name the face presented or provide uniquely identifying information (e.g. movie roles or political positions). Afterward we asked the participants whether they had substantial exposure to the faces they did not identify correctly.

**Table 1**

Scores on low-level visual tasks from the Birmingham Object Recognition Battery. Control scores are taken from the BORB manual.

	Length	Size	Orientation	Position of Gap
F19	29	27	23	36
F24	27	29	22	35
F54	25	27	26	35
F61	26	28	27	35
M33	27	29	24	35
M41	28	29	29	39
M57	27	28	27	37
Control mean	26.9	27.3	24.8	35.1
Control SD	1.6	2.4	2.6	4.0



**Fig. 1.** Face memory. Panel A: Prosopagnosic and control performance with famous faces. The x-axis shows the number of celebrities from our set of 60 that each participant reported substantial exposure to. The y-axis shows how many faces from that set were correctly identified. Panel B: Prosopagnosic and control scores on the Cambridge Face Memory Test. Prosopagnosics scores are shown in gray. There were 72 items and each item had three choices so chance performance is 24.

Because of the range of ages and backgrounds of the prosopagnosics, we used three different control groups tailored to the age and nationality of each subject. The eight American controls for M57 had an average age of 63.8 years ( $SD = 6.1$ ), and they averaged 52.6/60 ( $SD = 6.6$ ) correct identifications. Seventeen university age controls in the UK (average age = 19.8,  $SD = 1.4$ ) were compared to F18 and they averaged 51.4/60 ( $SD = 9.6$ ). Sixteen middle-aged UK adults (average age = 44.1,  $SD = 8.0$ ) were compared to the older UK prosopagnosics, and their average score was 47.3/60 ( $SD = 6.2$ ).

Fig. 1A plots the control and prosopagnosic scores on the famous face test. All the prosopagnosics scored poorly with famous faces and were a minimum of 2.5SDs below the mean for their control group. All of the prosopagnosics reported typical exposure to the celebrities, except F54 and F61. However, both identified less than half of the faces they reported exposure to so it appears that limited exposure is unlikely to account fully for their poor scores.

#### 4.2.2. Cambridge Face Memory Test (CFMT)

Because exposure to famous faces varies among the participants, we also examined their face memory using unfamiliar faces so that exposure was identical for

all participants. In the CFMT (Duchaine & Nakayama, 2006a,b), participants must recognize images of six target faces. Each target face was introduced by presenting participants with three different study views (left 3/4 profile, frontal, right 3/4 profile) for 3 s each. Immediately after presentation of the three study images for a particular target face, participants were presented with three forced choice items, which consisted of one of the study images paired with two other faces in the same pose. This study and test cycle was repeated for all six target faces. Thus, the introduction consisted of 18 items (6 faces  $\times$  3 test items per face). After this introductory phase, participants were tested with 54 forced choice items. Each item contained a novel view of one of the target faces and two non-target faces with the same pose and lighting condition. The first 30 items with novel views of the targets showed normal photographs, but noise was added to the final 24 items to make them more difficult.

Of the 72 items, 20 middle-aged controls (average age = 45.1,  $SD = 9.1$ ) averaged 59.7 ( $SD = 7.6$ ) items correct. Fig. 1B displays the scores for each prosopagnosic and control. All the prosopagnosics were out of the normal range and more than two standard deviations below the control mean. Not surprisingly, the means for the controls and prosopagnosics (35.9,  $SD = 5.3$ ) were significantly different ( $t(32) = 10.0, p < .001$ ).

#### 4.2.3. Cambridge Face Perception Test (CFPT)

On each item, participants were presented with a 3/4 profile view of a male target face above frontal views of six male test faces. Participants had 1 min to sort the test faces in terms of their similarity to the target. Each test face was a computer-morphed image, prepared by blending a frontal view of the target face with a frontal view of another face. The six test faces in each item were taken from six different morphed continua. Two steps were taken to systematically vary the similarity of each test face in an item to the target face. First, pilot subjects ranked the similarity of six different faces that were then morphed with the target face. The most similar test face was then prepared by morphing (i.e., blending) 88% of the target face with 12% of the face rated as most similar to the target face. The next most similar test faces contained 76% of the target and 24% of the next most similarly rated face, and so on, such that the other four other test faces contained 64%, 52%, 40%, and 28% of the target face blended with the remaining most to least similar faces. Eight different items were created and all used different target faces. Each item was presented upright once and inverted once. Upright and inverted items were intermixed, with the upright version occurring first half the time. One upright practice item and one inverted practice item were presented at the start of the test. Participants sorted the test faces by clicking on a face and then indicating where that face should be positioned by clicking in the area between two cards. The chosen face was then moved by the program to the desired location.

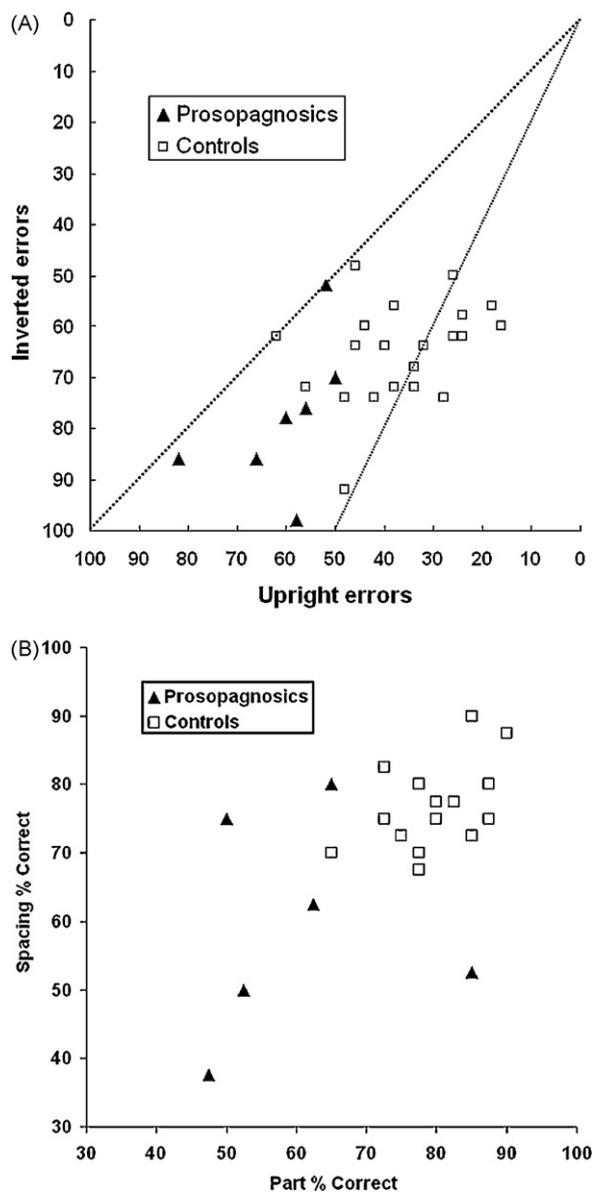
Scores for each item were computed by summing the deviations from the correct position for each face. For example, if a face was one position from its correct position, that was one error. If three positions away, that was three errors. Scores for each of the eight upright items and each of the eight inverted items were added to determine total number of upright and inverted errors. Chance performance with items of one orientation (upright or inverted) would result in 94 errors.

Fig. 2A displays upright and inverted errors for each control and prosopagnosic. Twenty-one age-matched controls (average age = 46.5,  $SD = 8.5$ ) showed a robust inversion effect. Fig. 2A shows that most of the controls clustered around the line further to the right in the figure, which displays scores with twice as many inverted errors as upright errors. Controls averaged 36.7 errors ( $SD = 12.2$ ) on the upright sorts while their inverted average was 65.0 errors ( $SD = 9.8$ ).

The prosopagnosics' scores are shifted primarily to the left in Fig. 2A, because they made far more upright errors than controls yet they made only slightly more inverted errors. Except for two controls who scored poorly, all the prosopagnosics scored worse than all the controls on the upright items. An ANOVA found significant effects for orientation ( $F(1,26) = 67.7, p < .001$ ) and group ( $F(1,26) = 20.6, p < .001$ ), but the interaction between orientation and group fell short of significance ( $F(1,26) = 3.1, p = .09$ ). For upright trials, prosopagnosics averaged 60.6 errors ( $SD = 10.8$ ), and their average was significantly different from the age-matched control group ( $t(26) = 4.60, p < .001$ ). All prosopagnosics did poorly with upright trials, with  $-1.1SD$  being the best individual z score. Their inverted average of 78.0 errors ( $SD = 10.8$ ) was also significantly worse than control inverted average ( $t(26) = 2.86, p = .01$ ).

#### 4.2.4. Discrimination of face parts and face part spacing

Our next test examined perception of face parts and face part spacing using a task used in previous experiments (Duchaine, Yovel, & Nakayama, 2007; Pitcher, Walsh, Yovel, & Duchaine, 2007; Yovel & Kanwisher, 2004; Yovel & Duchaine, 2006). Participants were sequentially presented with two faces for 500 ms each, and they judged whether the two faces were identical or different (Yovel & Duchaine, 2006). Forty trials consisted of pairs of identical images while 40 consisted of pairs of different images. There were two types of different trials. Faces with varied part spacing were created by manipulating the horizontal distance between the eyes and the vertical distance between the nose and mouth. Faces with varied parts were created by pasting in different eyes and mouths. Importantly, parts in the spacing variants were the same, and the spacing in the part variants was the same. This task was referred to as the Ann-S task by Yovel and Duchaine (2006). F24, however, was tested with a comparable task using a different face (Alfred) (Yovel & Duchaine, 2006; Yovel & Kanwisher, 2004). Her scores on the Alfred face were 55% for part discriminations and 60% for spacing discriminations. The control part average was 78.4% ( $SD = 9.6$ ) and the spacing average was 79.1% ( $SD = 10.0$ ) so both of her scores are very poor.



**Fig. 2.** Face perception. Panel A: Individual prosopagnosic and control scores on Cambridge Face Perception Test. The line running between the corners indicates scores in which upright and inverted errors are equivalent and the other line shows scores in which inverted errors are double upright errors. Panel B: Scores for controls and prosopagnosics on the part and spacing discrimination task. All the prosopagnosics scored more than two standard deviations below the control mean on one of the tests.

F24's results on the Alfred face are not included in the figure displaying the results for the Ann task (Fig. 2B).

The discrimination abilities of the six prosopagnosics who did the Ann task were compared to 15 age-matched controls (age range: 18–54). Fig. 2B shows that the prosopagnosics scored much more poorly than controls on both the part and spacing discrimination. The prosopagnosics showed a significant deficit in discrimination of the faces relative to the controls (59.6% vs. 78.3%,  $F(1,20) = 27.06, p < .001$ ). Like Yovel and Duchaine (2006), both prosopagnosics and controls showed no difference between their performance on the spacing (DPs = 59.6%, Controls = 76.9%) and part (DPs = 59.6%, Controls = 79.7%) discrimination tasks. Thus, the main effect of type (spacing or part) ( $F(1,20) = .44, p = .51$ ) and the interaction of group and type ( $F(1,20) = .72, p = .72$ ) were not significant. Inspection of the prosopagnosics' scores shows that each prosopagnosic had one score out of the normal range and four out of seven were at chance ( $\leq 52.5\%$ ) on one discrimination.

#### 4.3. Gaze perception

Having demonstrated that the prosopagnosics have deficits with facial identity perception and memory, we next assess how they perform with gaze perception

(Jenkins et al., 2006). First, we will test their gaze acuity in the absence of adaptation to a particular gaze direction. Then we will adapt to rightward and leftward gaze and examine whether they show the adaptation effects comparable to controls.

#### 4.4. Participants

Sixteen age-matched controls (average age = 43.9, SD = 16.4) were compared to the seven prosopagnosic participants (average age = 41.3, SD = 16.6).

#### 4.5. Baseline gaze acuity

##### 4.5.1. Method

Methods were identical to those used in Jenkins et al. (2006). The 60 color photographs used in the gaze acuity test consisted of 12 young adults displaying each of five gaze angles. The angles of gaze were 10° left (L10), 5° left (L05), straight ahead (S00), 5° right (R05), and 10° right (R10). The faces were presented in a black elliptical mask subtending a visual angle of approximately 12.6° vertically and 7.7° horizontally from the 60 cm viewing distance (see Fig. 3 for examples).

Fig. 3 displays the procedure in the baseline phase (phase one in Fig. 3). Participants were presented a fixation point for 750 ms, one of the 60 test faces for 1500 ms, and then a blank screen for 1000 ms. Participants responded with key presses to "1", "2", or "3" to indicate whether the model was gazing to the observer's left, straight on, or to the observer's right.

##### 4.5.2. Results

Fig. 4 displays the mean percentage of straight responses at each of the gaze angles for controls and prosopagnosic groups. The performance of the two groups was nearly identical. Both had high accuracy for straight gaze and gaze 10° left and right but often mistakenly classified 5° left and right stimuli as straight. An ANOVA with gaze angle (L10, L05, S00, R05, R10) and group (controls, prosopagnosics) as factors demonstrated gaze angle had a significant effect on the proportion of straight responses ( $F(4,84) = 130.5, p < .001$ ). As Fig. 4 shows, the comparison between controls and prosopagnosics was far from significant ( $F(1,21) = .095, p = .76$ ) as was the interaction ( $F(4,84) = .129, p = .98$ ).

#### 4.6. Gaze discrimination after adaptation to rightward and leftward gaze

##### 4.6.1. Method

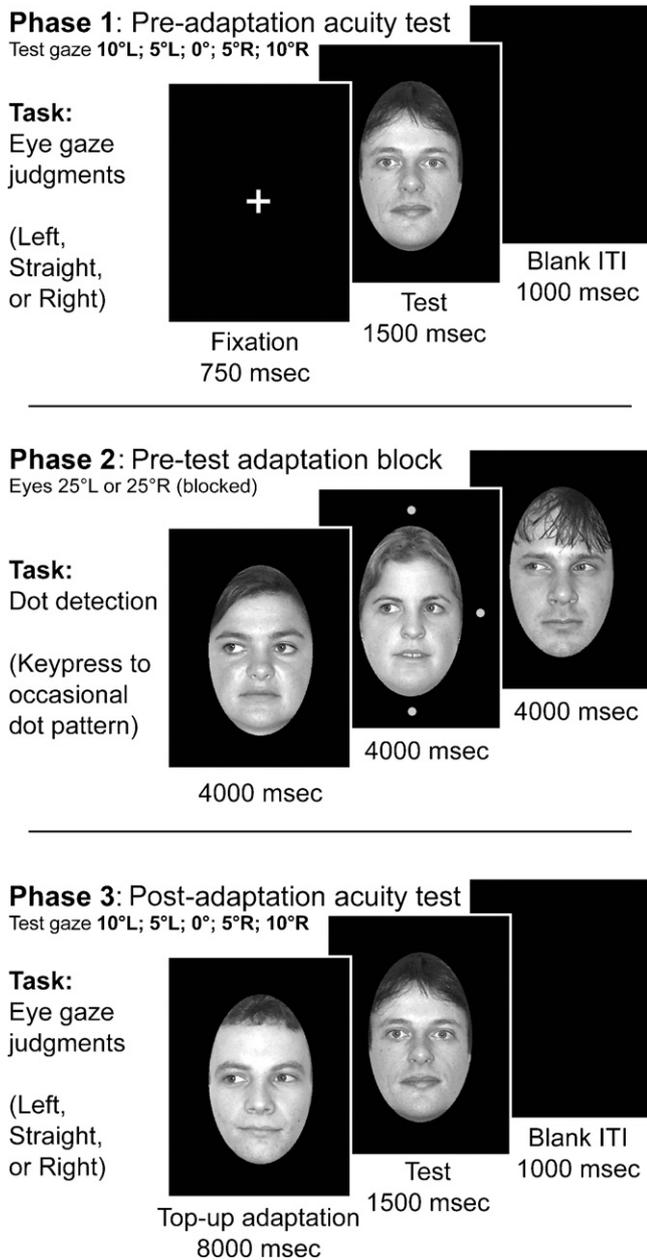
Half the participants were first adapted to rightward gaze and then tested whereas the other half were adapted to leftward gaze first and then tested. After the initial block, they were adapted in the opposite direction and tested again. In the pre-test adaptation phase (phase 2 in Fig. 3), participants viewed photographs of the 12 models looking either 25° to the right or 25° to the left. To guard against low-level adaptation effects, the adapting stimuli were twice the size of the test stimuli. The 12 adapting stimuli were cycled six times with each adapting stimulus presented for 4 s (approximately 5 min) (see Fig. 3). To maintain attention during this phase, four green dots surrounding the face flashed for 200 ms on 5% of the adapting trials and participants were instructed to press the space bar as quickly as possible if the dots appeared.

Following the pre-test adaptation phase was the post-adaptation gaze acuity test (phase three in Fig. 3). It contained the same test trials as the baseline acuity test, but each test trial was preceded by an 8 s top-adaptation stimulus. The top-up stimulus showed one of the faces seen in the adaptation phase, and like those faces, it was twice the size of the test faces. The identity was always different from the test face that immediately followed it. "Respond" was written above and below each test face so participants knew which face required a response.

##### 4.6.2. Results

Figs. 5 and 6 show that the mean percentage of straight responses for each gaze angle following leftward and rightward adaptation did not differ between controls and prosopagnosics. This was confirmed by a three-way ANOVA with group, gaze angle, and adaptation condition (baseline, left adapted, right adapted) as factors. Group was not significant ( $F(1,21) = .044, p = .835$ ) nor was the interaction between group and gaze angle ( $F(4,84) = .109, p = .979$ ), group and adaptation condition ( $F(2,42) = .748, p = .480$ ), or the three-way interaction between group, gaze angle, and adaptation condition ( $F(8,168) = .82, p = .588$ ). As expected, significant effects were found for adaptation condition ( $F(2,42) = 30.53, p < .001$ ), gaze angle ( $F(4,84) = 205.69, p < .001$ ), and these two factors interacted ( $F(8,168) = 55.05, p < .001$ ).

We carried out planned ANOVAs comparing the effect of group and comparing the effect of rightward or leftward adaptation to baseline at particular gaze angles. These analyses reinforce the findings above indicating strong effects of adaptation in the expected direction. Adaptation to rightward gaze had a strong effect on all gaze angles except L10 after Bonferroni correction (L05:  $F(1,21) = 10.06, p = .05$ ; S00:  $F(1,21) = 15.96, p = .01$ ; R05:  $F(1,21) = 40.26, p < .01$ ; R10:  $F(1,21) = 72.60, p < .01$ ). The same comparison for leftward adaptation found significant effects at gaze angles at L05 and L10 (L05:  $F(1,21) = 25.61, p < .01$ ; L10:  $F(1,21) = 96.49, p < .01$ ). Group and the interaction of group and adaptation condition were not significant at any of these gaze angles. These adaptation effects are similar to those seen in previous studies (Calder et al., 2007; Jenkins et al., 2006).

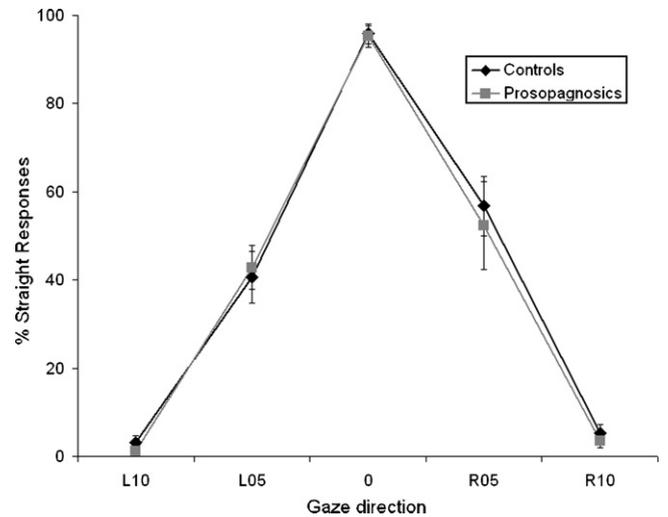


**Fig. 3.** Trial events and example stimuli in the baseline and adaptation gaze tasks. In the baseline task (Phase One), participants made key-press judgments concerning the direction of seen gaze (left, right, or straight ahead). In the pre-test adaptation phase (Phase Two), images twice the size of the test images were presented with eyes consistently averted in one direction. Participants passively viewed these averted-gaze stimuli for 5 min while monitoring for an occasional dot pattern. Immediately afterward, the gaze-acuity test was repeated, with top-up adaptation displays interleaved (Phase Three). Participants then repeated the gaze-acuity test after adapting to gaze in the opposite direction. ITI = intertrial interval; L25 = 25° left; L10 = 10° left; L05 = 5° left; S00 = straight ahead; R05 = 5° right; R10 = 10° right; R25 = 25° right.

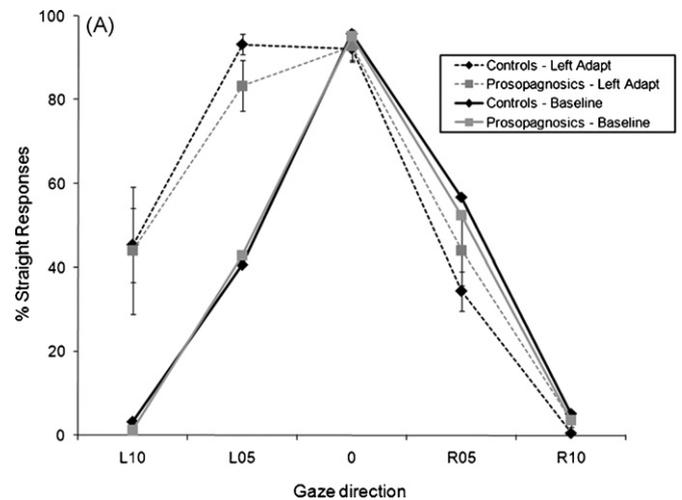
The figures display the proportion of straight responses because that best captures the adaptation effect. However subjects made left, right, or straight responses so display of the percentage of straight responses does not reveal whether non-straight responses were left or right. We have presented this data in the Appendix by showing the proportion of each response (left, straight, right) for each gaze probe in each condition. It shows that participants in both groups made very few left responses to right gaze probes or right responses to left gaze probes.

**5. Discussion**

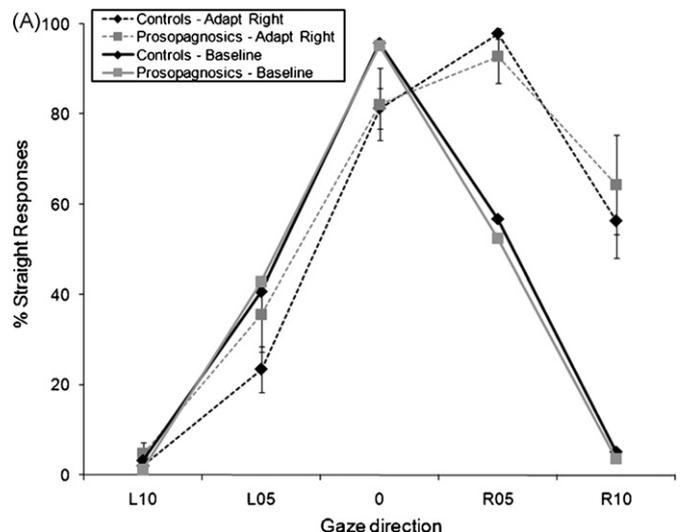
Leading models of face processing propose that the perception of facial identity and gaze are represented by different mechanisms.



**Fig. 4.** Baseline accuracy. This figure displays the average number of straight responses for each gaze direction for prosopagnosics and controls. Errors bars show the standard error of the mean.



**Fig. 5.** Performance after adaptation to leftward gaze. This figure shows the percentage of straight responses at each gaze direction for both groups along with the baseline data from Fig. 4 for comparison. Errors bars display the standard error of the mean.



**Fig. 6.** Performance after adaptation to rightward gaze. Percentage of straight responses at each gaze direction for both groups is shown along with the baseline data from Fig. 4 for comparison. Errors bars show the standard error of the mean.

Although neuroimaging and neurophysiological findings support this distinction, no previous neuropsychological cases have shown a dissociation between these two abilities. Our prosopagnosic participants however show that deficits with identity perception can be coupled with normal gaze acuity. Like past studies (Calder et al., 2007; Calder, Jenkins, Cassel, & Clifford, 2008; Jenkins et al., 2006), controls showed strong adaptation effects following adaptation to eyes gazing rightward and leftward. Post-adaptation performance revealed normal adaptation effects in all of the prosopagnosics, indicating that they represent gaze information in the same way subjects with normal face processing do.

The normal gaze perception in our prosopagnosic sample contrasts with the impairments seen previously in the two acquired prosopagnosics (Campbell et al., 1990; Perrett et al., 1988) and one developmental prosopagnosic (Campbell et al., 1990). Those three prosopagnosics showed clear impairments on a discrimination task in which subjects chose which of two sequentially presented faces showed straight gaze. Gaze perception then appears to be similar to other face processing abilities such as expression recognition, gender discrimination, and trait judgments in that some prosopagnosics show normal performance while others show impairments (Duchaine & Nakayama, 2006a,b). Note however that the task used in the present study included gaze judgments from faces in which head direction was always straight so that participants only had to use eye information. The previous studies required discrimination of gaze direction from heads in three positions. This more complex task requires representation of head direction, eye position, and the integration of these representations, and it will be worthwhile to explore each of these abilities in neuropsychological participants in future work.

The dissociation between impaired identity perception and normal gaze perception fits nicely with models proposing that these two abilities depend on separate mechanisms. In the model proposed by Haxby et al. (2000), identity and other invariant aspects of faces are processed in the fusiform gyrus whereas gaze and other changeable aspects of faces are represented in the STS. Given that we do not know the neural locus of our prosopagnosic participants' impairments with identity, our results do not provide evidence about the regions involved in identity and gaze perception but our results do support their cognitive dissociability. Considerable evidence points to the STS as a key region for gaze processing, and our results suggest that STS has developed normally in the developmental prosopagnosics and was spared in the acquired case.

fMRI measures of adaptation are used regularly to investigate impaired face processing (Avidan, Hasson, Malach, & Behrmann, 2005; Schiltz et al., 2006; Williams, Berberovic, & Mattingley, 2007), but behavioral performance after adaptation also appears to be a promising means to investigate face processing in neuropsychological participants. Neuropsychological tests sometimes allow test-takers to score normally using alternative strategies that do not rely on the ability researchers are attempting to measure (Duchaine & Nakayama, 2004; Duchaine & Weidenfeld, 2003; Nunn, Postma, & Pearson, 2001; Yovel & Duchaine, 2006). For example, it is difficult to rule out the possibility that prosopagnosic participants in the

baseline condition were making their decision based simply on the position of some aspect of the eye rather than perceiving the gaze information in the natural way that normal participants do. However, the demonstration of normal adaptation in the prosopagnosics provides additional and arguably stronger evidence of normal gaze perception, because it seems highly unlikely that the use of an alternative method to judge gaze direction would produce nearly equivalent adaptation effects to those shown by the controls. The one other face processing study that used a similar approach investigated identity processing in autism (Pellicano, Jeffery, Burr, & Rhodes, 2007). The autistic participants showed a normal ability to discriminate between two faces, but discrimination after adaptation revealed that they showed much weaker identity adaptation than controls and so indicated that they do not represent identity normally. Many aspects of face processing produce robust adaptation effects (Fang & He, 2005; Ng, Ciaramitaro, Anstis, Boynton, & Fine, 2006; Webster, Kaping, Mizokami, & Duhamel, 2004; Webster & MacLin, 1999) so post-adaptation performance can provide a valuable additional measure in a range of neuropsychological studies.

These results add to the list of face processing abilities that have dissociated from identity perception in prosopagnosia. In addition to gaze perception, these abilities include face detection (Garrido, Duchaine, & Nakayama, 2008), expression recognition (Bentin, DeGutis, D'Esposito, & Robertson, 2007; Duchaine, Parker, & Nakayama, 2003; Humphreys, Avidan, & Behrmann, 2007; Riddoch, Johnston, Bracewell, Boutsen, & Humphreys, 2008), trustworthiness judgments (Todorov & Duchaine, 2008), and long-term memory for faces (Tippett, Miller, & Farah, 2000). These dissociations are consistent with fMRI and neurophysiological studies indicating that different types of face processing rely on different areas (Calder et al., 2007; Engell, Haxby, & Todorov, 2007; Haxby et al., 2000; Rotshtein, Henson, Treves, Driver, & Dolan, 2005; Winston et al., 2004; Winston, O'Doherty, Kilner, Perrett, & Dolan, 2007). Understanding how these areas processes gaze and other aspects of faces is a major challenge, and the use of adaptation measures in neuropsychological subjects seems likely to contribute to this effort.

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## Appendix A. Mean proportion of left, direct, and right responses for each group to the five probe gaze directions (10° Left, 5° Left, 0°, 5° Right, and 10° Right) in the baseline and adaptation conditions

Response type by condition	10° left		5° left		0° (direct)		5° right		10° right	
	M	SD	M	SD	M	SD	M	SD	M	SD
Left responses										
Controls										
Baseline	0.97	0.06	0.59	0.23	0.04	0.09	0	0	0	0
Left adapt	0.55	0.35	0.07	0.10	0.01	0.03	0	0	0	0
Right adapt	0.98	0.05	0.77	0.20	0.19	0.18	0	0	0	0
Prosopagnosics										
Baseline	0.99	0.03	0.57	0.13	0.04	0.04	0	0	0	0

## Appendix A (Continued)

Response type by condition	10° left		5° left		0° (direct)		5° right		10° right	
	M	SD	M	SD	M	SD	M	SD	M	SD
Left adapt	0.56	0.40	0.17	0.16	0	0	0	0	0	0
Right adapt	0.95	0.07	0.64	0.22	0.17	0.21	0.02	0.06	0	0
Straight responses										
Controls										
Baseline	0.03	0.06	0.41	0.23	0.96	0.09	0.57	0.27	0.05	0.08
Left adapt	0.45	0.35	0.93	0.10	0.92	0.11	0.34	0.19	0.01	0.02
Right adapt	0.02	0.05	0.23	0.20	0.81	0.18	0.98	0.05	0.56	0.33
Prosopagnosics										
Baseline	0.01	0.03	0.41	0.14	0.93	0.09	0.52	0.24	0.03	0.04
Left adapt	0.50	0.41	0.85	0.16	0.91	0.11	0.40	0.24	0.03	0.04
Right adapt	0.04	0.06	0.35	0.20	0.84	0.21	0.94	0.15	0.66	0.27
Right responses										
Controls										
Baseline	0	0	0	0	0	0	0.43	0.27	0.95	0.08
Left adapt	0	0	0	0	0.07	0.11	0.66	0.19	0.99	0.02
Right adapt	0	0	0	0	0	0	0.02	0.05	0.44	0.33
Prosopagnosics										
Baseline	0	0	0	0	0.01	0.03	0.48	0.26	0.96	0.04
Left adapt	0	0	0	0	0.07	0.10	0.56	0.22	0.96	0.04
Right adapt	0	0	0	0	0.01	0.03	0.05	0.09	0.36	0.29

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