Available online at www.sciencedirect.com

### **ScienceDirect**

Journal homepage: www.elsevier.com/locate/cortex

### **Research report**

## Seeing the eyes in acquired prosopagnosia



<sup>a</sup> Human Vision and Eye Movement Laboratory, Departments of Medicine (Neurology), Ophthalmology and Visual Sciences, University of British Columbia, Vancouver, Canada <sup>b</sup> Department of Psychology, Dartmouth University, Dartmouth, USA

#### ARTICLE INFO

Article history: Received 24 July 2015 Reviewed 6 November 2015 Revised 18 January 2016 Accepted 27 April 2016 Action editor Gus Buchtel Published online 24 May 2016

Keywords: Acquired prosopagnosia Eye region Face feature Fusiform face area

#### ABSTRACT

Case reports have suggested that perception of the eye region may be impaired more than that of other facial regions in acquired prosopagnosia. However, it is unclear how frequently this occurs, whether such impairments are specific to a certain anatomic subtype of prosopagnosia, and whether these impairments are related to changes in the scanning of faces.

We studied a large cohort of 11 subjects with this rare disorder, who had a variety of occipitotemporal or anterior temporal lesions, both unilateral and bilateral. Lesions were characterized by functional and structural imaging. Subjects performed a perceptual discrimination test in which they had to discriminate changes in feature position, shape, or external contour. Test conditions were manipulated to stress focused or divided attention across the whole face. In a second experiment we recorded eye movements while subjects performed a face memory task.

We found that greater impairment for eye processing was more typical of subjects with occipitotemporal lesions than those with anterior temporal lesions. This eye selectivity was evident for both eye position and shape, with no evidence of an upper/lower difference for external contour. A greater impairment for eye processing was more apparent under attentionally more demanding conditions. Despite these perceptual deficits, most subjects showed a normal tendency to scan the eyes more than the mouth.

We conclude that occipitotemporal lesions are associated with a partially selective processing loss for eye information and that this deficit may be linked to loss of the right fusiform face area, which has been shown to have activity patterns that emphasize the eye region.

© 2016 Elsevier Ltd. All rights reserved.

<sup>1</sup> Neuro-ophthalmology Section K, VGH Eye Care Centre, Vancouver, British Columbia, Canada. http://dx.doi.org/10.1016/j.cortex.2016.04.024







<sup>\*</sup> Corresponding authors. Human Vision and Eye Movement Laboratory, Departments of Medicine (Neurology), Ophthalmology and Visual Sciences, University of British Columbia, Vancouver, Canada.

E-mail addresses: raikap@gmail.com (R. Pancaroglu), jasonbarton@shaw.ca (J.J.S. Barton).

<sup>0010-9452/© 2016</sup> Elsevier Ltd. All rights reserved.

#### 1. Introduction

Acquired prosopagnosia is a selective visual agnosia in which the ability to recognize familiar faces or to learn new faces is lost (Barton, 2003). The nature of the impairment that leads to problems recognizing faces remains a topic of investigation. As with all complex processes, face recognition involves several cognitive operations (Bruce & Young, 1986) and an extensive cerebral network (Fox, Iaria, & Barton, 2009). Hence acquired prosopagnosia is likely a family of disorders with variants that differ in their functional and structural bases (Barton, 2008; Davies-Thompson, Pancaroglu, & Barton, 2014).

In some, particularly those with fusiform lesions, the impairment is likely perceptual, a difficulty in perceiving the subtle differences that distinguish one face from another (Barton, 2008). However, there is considerable debate about what this apperceptive defect entails. Some suggest that holistic face processing is lost for some parts of the face (Bukach, Bub, Gauthier, & Tarr, 2006; Busigny & Rossion, 2011; Kimchi, Behrmann, Avidan, & Amishav, 2012), with the possible consequence of reliance on a local feature-by-feature strategy (Bukach et al., 2006; Levine & Calvanio, 1989). Others have demonstrated an inability to process the configuration of facial features (Barton, 2008; Barton, Press, Keenan, & O'Connor, 2002; Joubert et al., 2003).

Another interesting aspect is the possibility that the prosopagnosic impairment may affect the processing of some parts of the face more than others. There is evidence that not all aspects of the face contribute equally to face identification. The eye region contain the most diagnostic information for face identification (Sadr, Jarudi, & Sinha, 2003; Vinette, Gosselin, & Schyns, 2004) and can be used to discriminate faces (Sekuler, Gaspar, Gold, & Bennett, 2004). Behavioral performance in face identity tasks most reliably correlates with horizontal contour information from the eye region (Pachai, Sekuler, & Bennett, 2013). Healthy subjects look most at the eyes when recognizing faces and scan the upper facehalf more than the lower half (Barton, Radcliffe, Cherkasova, Edelman, & Intriligator, 2006; Henderson, Williams, & Falk, 2005), and studies of cue saliency show that the eye region is particularly emphasized (Shepherd, Davies, & Ellis, 1981). Models of face scanning suggests that looking near the eyes is optimal for face recognition (Peterson & Eckstein, 2012).

Ironically, the early seminal description of prosopagnosia (Bodamer, 1947) recounted the anecdotal observation of the two patients that they were attracted to the eyes (Ellis & Florence, 1990). Likely the first experimental observation of disproportionate difficulty perceiving the eyes in acquired prosopagnosia was that of two prosopagnosic subjects who had more trouble matching eyes than mouths to whole faces (Gloning & Quatember, 1966; Gloning, Gloning, Hoff, & Tschabitscher, 1966). This issue was not examined further until recently. One study of four prosopagnosic subjects with fusiform lesions found that discrimination of facial configuration was more consistently impaired in the eye than the mouth region (Barton et al., 2002). Subjects LR and HH were impaired in perceiving changes of the eyes but not the mouth, whether those were changes in spatial position, a feature swap or a change in feature size (Bukach et al., 2006; Bukach,

Le Grand, Kaiser, Bub, & Tanaka, 2008). Subject PS had difficulty discriminating changes in eye brightness or spatial position (Ramon & Rossion, 2010; Rossion, Kaiser, Bub, & Tanaka, 2009) and the Bubbles technique showed that she relied more on the mouth and external contours than the eyes for facial identity (Caldara et al., 2005). Subject GG was studied with the same perceptual discrimination tests, with similar findings (Busigny, Joubert, Felician, Ceccaldi, & Rossion, 2010). Also, in developmental prosopagnosia there is some evidence that impaired holistic processing is more severe for the eye than the mouth region (DeGutis, Cohan, Mercado, Wilmer, & Nakayama, 2012).

These cases raise several issues. The first is how common or uniform is this apparent selectivity of impaired eye processing in prosopagnosia. A review of 10 cases, including the four previously reported (Barton et al., 2002), noted impaired perception of eye configuration and normal perception of mouth configuration in three subjects (Barton, 2008). All three had right occipitotemporal lesions, as did all the cases above, with the exception of LR. Given that a variety of lesions can cause prosopagnosia (Barton, 2008), one question is whether impaired eye perception is specific to right occipitotemporal lesions. Indeed, a neuroimaging study of regional saliency in healthy subjects found that the fusiform face area showed a feature-salience hierarchy that emphasized the eyes and correlated with human perceptual efficiency, which was best for the eyes (Lai, Pancaroglu, Oruc, Barton, & Davies-Thompson, 2014).

A second question concerns the type of information processing that shows a selective vulnerability in the eye region. While most reports show that the processing of the spatial position of the eye is impaired, a number also show that ocular feature properties are affected. Subjects do not perceive changes from swapping of the eyes (Bukach et al., 2006), altering eye brightness (Busigny et al., 2010; Ramon & Rossion, 2010) or eye size (Bukach et al., 2008; Busigny et al., 2010; Rossion et al., 2009). Also, one can ask whether this effect is limited to an eye/mouth contrast or is part of a more general upper/lower face contrast, by examining the perception of external facial contour. In healthy subjects the perception of external contours is just as vulnerable to the inversion effect as is the perception of facial features (Malcolm, Leung, & Barton, 2004). Figure 4 of the Bubbles study (Caldara et al., 2005) suggests that subject PS uses the external contour of the lower but not the upper face.

A third question relates to the perceptual conditions under which this eye vulnerability emerges. Two reports found that some prosopagnosic subjects perform better or even normally when given blocks in which only one type of facial change is to be detected, than with blocks containing trials with many different changes (Barton et al., 2002; Ramon & Rossion, 2010). This suggests that the impairment is more evident when attention needs to be divided across the whole face. If so, this defect may be related to or interact with holistic mechanisms (Rossion et al., 2009; de Xivry, Ramon, Lefèvre, & Rossion, 2008).

Finally, there is the question of whether these perceptual deficits are accompanied by changes in the way faces are explored with eye movements. One potentially trivial explanation is that subjects do not attend to the eyes, which may be

evident as decreased fixations on the eyes. Reduced fixation of eves is found in subjects with autism spectrum disorders (Klin, Jones, Schultz, Volkmar, & Cohen, 2002; Yi et al., 2013), some of whom show impaired face perception (Barton et al., 2004). Others suggest that amygdala dysfunction in acquired prosopagnosia may biases fixations away from the eyes (Bukach et al., 2008). Empirically, two studies have shown that subject PS fixates more on the mouth and less on the eyes, compared to controls (Van Belle, De Graef, Verfaillie, Busigny, & Rossion, 2010; de Xivry et al., 2008), as does subject GG (Van Belle et al., 2011). However, four other subjects with acquired prosopagnosia have shown either normal scanpaths (Rizzo, Hurtig, & Damasio, 1987) or normal emphasis on the eye over the mouth region during face identification (Barton, Radcliffe, Cherkasova, & Edelman, 2007) or categorization of faces as normal upright faces (Le, Raufaste, & Demonet, 2003).

In this report, we studied face perception in a large cohort of subjects with acquired prosopagnosia, from a variety of lesions and etiologies. Our goal was to address the four issues identified above: 1) whether impaired processing of the eyes was specific to prosopagnosic subjects with fusiform lesions; 2) whether an eye processing deficit was found not only for their spatial relationship but also for their shape and external facial contours; 3) whether eye processing impairments were still present when attention was focused on the eye region, or only when conditions demanded attention to the whole face; and 4) whether they showed reduced fixation on the eyes.

#### 2. Materials and methods

#### 2.1. Participants

Protocols were approved by the institutional review boards of UBC and VGH. Written consent was taken from all subjects and healthy participants in accordance with the Code of Ethics of the World Medical Association, Declaration of Helsinki (Rickham, 1964).

Subjects with acquired prosopagnosia were recruited from the website www.faceblind.org. All had a neuro-

Table 1 – Patient background data.

ophthalmological history and examination, including Goldmann perimetry (Table 1). All had corrected Snellen visual acuity of at least 20/30 in the better eye. All complained of impaired face recognition in daily life. None had complaints of mistaking one type of object for another, and all were able to identify real objects and objects in line drawings during the clinical examination.

Subjects underwent a battery of neuropsychological tests for handedness, general intelligence, executive function, memory, attention, visual perception and language skills (Supplementary Table 1). The diagnosis of prosopagnosia was supported by performance on face recognition tests (Table 2). Subjects were impaired on at least one of two tests of familiarity for recently viewed faces, the Cambridge Face Memory Test (Duchaine & Nakayama, 2006) or the face component of the Warrington Recognition Memory Test (Warrington, 1984), while performing normally on the word component of the latter. Face recognition was evaluated with a Famous Faces Test (Barton, Cherkasova, & O'Connor, 2001). Although not part of the diagnostic criteria for prosopagnosia, subjects were also assessed for pereptual discrimination of faces with the Benton Face Recognition Test (Benton & Van Allen, 1972) and the Cambridge Face Perception Test (Duchaine, Germine, & Nakayama, 2007), and also for face imagery (Barton & Cherkasova, 2003).

All prosopagnosic subjects had structural (Fig. 1) and functional magnetic resonance imaging (Fig. 2. Supplementary Table 2) to localize the core face-processing network, using the HVEM dynamic face localizer protocol (Fox et al., 2009), as described in a recent report (Hills, Pancaroglu, Duchaine, & Barton, 2015). The nomenclature for our prosopagnosic subjects follows the evidence for tissue loss or hypointensity on T1-weighted images. Lesions mainly anterior to the anterior tip of the middle fusiform sulcus (Weiner et al., 2014) were designated as anterior temporal (AT) and those posterior to it as inferior occipitotemporal (IOT). B-ATOT2 had bilateral fusiform lesions and a right anterior temporal lesion, as well as posterior periventricular hyperintensities on FLAIR sequences. L-IOT2, who had resection of the left fusiform gyrus for epilepsy treatment, also had

Group Subject		Age at testing	Age at onset	Gender	Lesion	Visual fields	
Acquired prosopagnosia, inferior occipitotemporal	R-IOT1	56	37	М	Hemorrhage, AV malformation	LUQ	
	R-IOT4	62	61	М	Infarction	LUQ	
	B-IOT2	60	26	М	Subdural hematoma	BHH	
	L-IOT2	59	41	М	Left fusiform resection,	Full	
					right atrophy		
	B-ATOT1	46	14	F	HSV encephalitis	LUQ	
	B-ATOT2	23	10	F	HSV encephalitis	Full	
Acquired prosopagnosia,	R-AT2	34	25	F	HSV encephalitis	Full	
anterior temporal	R-AT3	37	30	М	HSV encephalitis	Full	
	R-AT5	60	32	F	Tumor resection	Full	
	B-AT1	25	21	М	HSV encephalitis	Full	
	B-AT2	47	24	F	Trauma, temporal	Full	
					resection		

M = male, F = female.

LUQ = left upper quadrantanopia, BHH = bilateral hemianopia.

HSV = herpes simplex virus.

	R-IOT1	R-IOT4	L-IOT2	B-IOT-2	B-ATOT1	B-ATOT2	R-AT2	R-AT3	R-AT5	B-AT1	B-AT2
FACES											
Face perception											
BFRT	45	46	31	38	41	37	47	38	33	45	40
CFPT	62	76	74	70	100	80	40	48	92	52	76
Familiarity											
Famous	1.96	1.29	.00	1.31	.00	.15	.65	.90	1.52	.36	.68
faces d'											
Face memory											
WRMT face	33	39	27	21	27	19	27	31	28	27	31
WRMT word	41	50	42	42	50	39	47	47	46	45	46
CFMT	44	27	21	24	30	24	33	31	35	30	31
Face imagery	82	84	41	86	60	48	73	49	81	а	50

#### Table 2 - Evaluation of face processing.

BFRT - Benton face recognition test.

WRMT – Warrington Recognition Memory Test.

CFMT – Cambridge face memory test.

Bold-italics text indicates an abnormal result.

<sup>a</sup> B-AT1 did not recognize enough celebrity names to perform the imagery test.

atrophy of the right fusiform gyrus and is grouped with the subjects with bilateral lesions (Fig. 2).

# 2.2. Experiment 1. Discrimination of feature position, shape and external contour

Subjects discriminated changes to either the configuration or the shape of the eyes or mouth, or to the external contour of the hairline or jawline, under different processing loads and attentional demands. In one condition, the six different changes were presented in six separate blocks and subjects were informed what type of change would be seen in that block. Hence subjects could focus their attention on this one facial property. In a second condition, two possible changes could occur in a block, in random order, but both in the same facial region. Thus, while they could not attend exclusively to one facial property, they could attend to one facial region. In the third condition, all six changes were presented in random order in one block.

#### 2.2.1. Subjects

All 11 prosopagnosia subjects participated, as did 12 healthy participants (8 females; mean age = 38, age range = 25-55) with no history of neurological disease or cognitive complaints.

#### 2.2.2. Procedure

This used the protocol of a previous study of inversion effects (Malcolm et al., 2004). Stimuli were generated from three males and three females. Target faces were created with changes in configuration, feature shape, or external contour, using Adobe Photoshop 5.5 (www.adobe.com) (Fig. 3). For configural changes, horizontal inter-ocular distance was reduced by 16 pixels, or the mouth was moved up 10 pixels. For feature shape, the eyes were elongated vertically by 14 pixels or the mouth by 18 pixels. For external contour, the hairline was elevated or the jaw line narrowed.

Subjects were shown three faces simultaneously in a triangular arrangement, with the left face 7% larger and the right face 14% larger than the top face, which spanned 3° in

height and 2.4° in width. Two faces were the unaltered originals, while the third was one of the targets, which had an equal likelihood of appearing at any of the three positions. The task was to indicate by keypress which was the target. Viewing time was unlimited.

Trials were presented using Superlab 1.71 (www.superlab. com). There were three viewing conditions. In the first, each block contained only one possible target type: hence all six targets were shown in six different blocks, each with 18 trials ('1-change condition'). In the second, there were two blocks of 36 trials, each with two possible target types in random order ('2-change condition'). In one there were changes to eye configuration or eye shape, in the other there were changes to mouth configuration or mouth shape. Subjects were informed about the face region where the change would occur. In the third condition, there was only one block of 108 trials, which showed all six change types in random order ('6-changes condition'). For all blocks in all conditions, subjects were instructed in advance what changes would occur. All subjects performed the blocks in the same order, as follows: 1-change (chin, eye position, eye shape, forehead, mouth shape, mouth position), 2-changes (upper, lower), 6-changes.

#### 2.2.3. Statistical analysis

Since visual field defects may affect response times, we focused on analyzing accuracy. The response times data are provided in Supplementary Table 3. Using JMP 10 (www.jmp. com), we first examined the control data with ANOVA with repeated measures. Because external contour was not examined in the 2-changes condition, we performed two analyses. The first omitted the external contour data and had factors of location (upper, lower), type of change (configuration, shape), and condition (1-change, 2-change, 6-change), with subject as a random effect. The second omitted the 2-changes data and had factors of location (upper, lower), type of change (configuration, shape, external contour), and condition (1-change, 6-changes). Significant interactions were examined with Tukey's honestly significant different (HSD) test.

We then analyzed the data of individual prosopagnosic subjects, deriving 95% prediction intervals from control data



Fig. 1 – Structural images of lesions. Axial T1-weight MRI of all subjects. Top six subjects have occipitotemporal lesions, while in the bottom five subjects the lesions are confined to the anterior temporal lobe.





Spatial relation

Feature size

External contour

Fig. 3 – Examples of target faces used in experiment 1. Top row shows faces with changes in the upper face, bottom row shows faces with changes in the lower face. Left images show configuration changes (reduced interocular distance, top; reduced nose-mouth distance, bottom), middle images show feature size changes (larger eyes, top; fatter lips, bottom), and right images show external contour changes (elevated hairline, top; narrower jaw, bottom).

to identify abnormality at a single-subject level. To contrast the degree of abnormality in upper versus lower face scores in a group analysis, control data were used to z-transform the prosopagnosia data. We used paired t-tests to examine the null hypothesis that z-scores did not differ between the eyes and mouth for each type of change in each condition.

#### 2.3. Experiment 2. Fixation analysis during face encoding and retrieval

#### 2.3.1. Subjects

Eight of the 11 prosopagnosic subjects participated: the exceptions were R-IOT1, B-ATOT1, and R-AT5. There were 20 healthy control subjects (10 female; mean age = 34.4, range 18-66) with no history of neurological disease or cognitive impairments, and corrected acuity of 20/30 or better.

#### 2.3.2. Apparatus

Subjects sat in a room with dim lighting, 34 cm away from the computer display, viewing the stimuli with both eyes. Head position was maintained by a chin rest. Eye movements were recorded by an Eyelink 1000 system (SR Research Ltd, Mississauga, Canada). Stimuli and trials were programmed in SR Research Experiment Builder 1.10.165. Stimuli were displayed on a white background on a high refresh-rate monitor at 140 Hz with a 1024 imes 768 pixel resolution.

#### 233 Stimuli

Thirty male faces from the KDEF face database were used (Lundqvist & Litton, 1998). Five faces were randomly selected as target identities. Two images of each target identity were used in the learning phase, one with neutral and the second with either sad or happy expression. The rest of the 25 facial identities were distractors, with randomly selected different facial expressions (6 neutral, 4 happy, 5 sad, 4 surprised, 4 angry, 1 afraid). All images were converted to gray scale and matched for luminance using Adobe Photoshop CS2 (www. adobe.com). Faces were cropped to remove external features, with a straight line at the top, and the natural contour elsewhere. The tip of the nose was placed at screen center. Faces were adjusted in size so that all stimuli spanned 23° in width and 27° in height: such large faces were used to ensure the classification accuracy for fixation position (Barton et al., 2006).

Fig. 2 – Functional imaging. Orange regions indicate core face regions activated during viewing of the dynamic face localizer, superimposed upon T1-weighted coronal images of subjects. Subjects with occipitotemporal lesions have absent right fusiform face area in common, most also not showing activation of the right occipital face area. Subjects with anterior temporal lesions show intact activation of all core face processing regions.

#### 2.3.4. Procedure

Subjects started with a 9-point grid calibration. In the Learning phase, subjects were shown the 10 images of the 5 target identities. Subjects were asked to memorize the identity of these targets. Each trial began with a fixation cross spanning 1.43° and located 7.1° above where the faces would appear. Subjects had to fixate within 2° of the cross for at least 100 msec for the trial to begin. After 1050 msec, one of the target faces appeared at the center of the screen. After subjects had studied it for as long as they wished, they pressed the space bar, the face disappeared and the fixation cross reappeared. Following fixation within 2° of the cross for at least 100 msec, and a delay of 1050 msec, the second image of the same identity was shown. After the subject pressed the space bar the next two trials for the next identity began. Failure in fixation resulted in re-calibration followed by resumption of the trial with unsuccessful fixation.

After a short break of less than 60 sec, subjects initiated the Recognition phase by pressing the space bar. Each trial began with the same fixation cross and requirement for fixation within 2° of the cross for at least 100 msec. After 1050 msec a face appeared at the center of the screen, and remained visible until the subject pressed either the left arrow if they believed that they had seen that person in the Learning phase, or the right arrow if they did not. There were 35 trials, 10 being the same images seen during the learning phase, and 25 distractor faces. Subjects were not told the number of targets shown in the recognition phase.

#### 2.3.5. Analysis

Responses in the recognition phase were first analyzed using signal detection theory to calculate discriminative power (d') and criterion bias (c'). Because the F-test for the equality of variances of the controls and the prosopagnosic subjects showed no difference for either d' [F(18,6) = 2.11, p = .18], or c' [F(18,6) = .83, p = .65], we used 2-sample t-tests for samples with equal variance to contrast controls and prosopagnosic subjects.

We used SR Research Eyelink Data Viewer 1.10.1 to analyze eye movements. In each trial viewing time was marked as the time between image onset on the screen and keyboard press, and analysis was limited to this interval. Facial regions of interest were defined for the eyes, mouth, upper face and lower face. The areas of these regions were adjusted so that they were equivalent, with both the eyes and the mouth regions having an area of 216° squared, and the upper and lower face 325° squared. We calculated the total duration of fixations spent in each region on each trial.

We compared the results from three 'phases': the learning phase, and targets and distractors separately from the recognition phase. As controls spent on average 9807 msec fixating each face in the learning phase, but only 3284 msec on each target and 2643 msec on each distractor face in the recognition phase, fixation data were log-transformed.

For control subjects, we used a repeated-measures ANOVA with phase (learning, target, distractor) and face-half (upper, lower) as main factors, and subject as a random effect. This was repeated replacing face-half with face-part (eyes, mouth). Interactions were examined with Tukey's HSD test. For prosopagnosic subjects we first examined total fixation duration for the entire face, comparing these to 95% prediction intervals derived from the control data to classify the results of individual prosopagnosic subjects as normal or abnormally prolonged.

We then calculated an Upper/Lower Face Index by dividing the difference between the fixation durations on the upper and the lower face by the sum of the two. We created a similar Eye/Mouth Index. 95% prediction limits were calculated from controls to characterize abnormality of individual prosopagnosic subjects. For a group analysis, we subjected these indices to a repeated-measures ANOVA, with group (control, occipitotemporal, anterior temporal) and phase (learning, target, distractor) as main factors, and subject as a random effect, examining effects with the Tukey's HSD test.

#### 3. Results

# 3.1. Experiment 1. Discrimination of feature position, shape and external contour

Control subjects easily detected the changes in all conditions, with mean accuracy above 94% for all subtests. The first ANOVA with repeated measures excluded the external contour trials, and showed an effect of condition [F(2,121) = 4.43, p < .014], with Tukey's HSD test showing that accuracy in the 6-changes condition was less than that in the 1-change and 2-changes conditions, while the latter two did not differ from each other. There was an interaction between condition and location [F(2,121) = 5.53, p < .005], with Tukey's HSD test showing better accuracy in the eye than mouth in only the 6-changes condition. Mouth accuracy was worse in the 6-changes than the 1 or 2-changes conditions, with no difference between the latter two, while eye accuracy was similar in all conditions.

The second ANOVA with repeated measures excluded the 2-changes condition. This showed an effect of condition [F(1,121) = 10.2, p < .002] due to more accurate responses in the 1-change condition, and an interaction of condition with location [F(1,121) = 6.17, p < .015]. Tukey's HSD test showing that lower-face accuracy was worse than upper-face accuracy in the 6 but not the 1-change condition. Conversely, accuracy in the 6-changes condition was worse in the lower than the upper face, with no difference between in the 1-change condition.

To summarize, controls showed an upper face (or eye) advantage emerging only during attention to multiple facial properties, without evidence that this is specific for one particular type of change.

The data for individual prosopagnosic subjects (Table 3) showed that all but one of the five anterior temporal subjects performed normally with all features in the 1-change condition, while this was true of only half of those with occipito-temporal lesions. In the 2-changes condition, three of the five anterior temporal subjects continued to perform normally with all features, while none of the occipitotemporal subjects did. In the 6-changes condition, the anterior temporal subjects began to have more difficulty. However, the occipitotemporal

subjects were now uniformly impaired for many features, particularly for eye shape and position, for which none obtained a normal score.

Comparisons of scores from the upper versus lower face in individual subjects revealed an interesting observation. While there were 23 instances where the upper face score was abnormal with a normal corresponding lower face score, there were only two instances where the reverse held, both in the 1change condition, for feature shape in R-IOT4 and for external contour in B-ATOT1.

When we plot the z-scores for discriminating the eye (upper) versus mouth (lower) changes (Fig. 4), the occipitotemporal subjects showed a trend for eye z-scores to be worse than mouth z-scores for feature position  $[-4.9 \pm 5.3$  for eye vs  $-1.5 \pm 4.1$  for mouth, t(5) = 1.59, p < .09], but not for feature shape or external contour. In the 2-changes condition, eye z-scores were worse than mouth z-scores for feature position  $[-20.2 \pm 13.6$  for eye vs  $-3.7 \pm 4.0$  for mouth, t(5) = 3.55, p < .01] but not feature shape. In the 6-changes condition, the eye disadvantage for feature position was even more significant  $[-20.6 \pm 8.2$  for eye vs  $-3.7 \pm 3.4$  for mouth, t(5) = 6.92, p < .0005], and there was now a similar eye disadvantage for feature shape  $[-15.8 \pm 9.4$  for eye vs  $-4.2 \pm 3.9$  for mouth, t(5) = 3.88, p < .01], but not for external contour.

In contrast, for the anterior temporal group, the mean eye and mouth z-scores was almost always similar, with only one exception, more difficulty with the eyes again for feature shape in the 2-changes condition  $[-7.6 \pm 10.1$  for eye vs  $-2.3 \pm 3.0$  for mouth, t(4) = 3.29, p < .02].

### 3.2. Experiment 2. Fixation analysis during face encoding and retrieval

#### 3.2.1. Behavioral results

As expected, prosopagnosic subjects had a lower mean d' of .52, compared to 1.79 for controls [t(24) = 3.08, p < .0052].

However, the mean criterion bias (c') did not differ between the groups, being .07 for both [t(24) = .006, p = .99]. Hence in this testing situation the prosopagnosics show lower discriminative ability but no bias towards stating that faces are unfamiliar or familiar when guessing (Fig. 5).

#### 3.2.2. Ocular motor results

In the analysis of face halves, ANOVA showed a main effect of phase [F(2,95) = 55.2, p < .0001]: Tukey's HSD test showed that controls spent more time looking at faces in the learning phase than at targets or distractors in the recognition phase. There was a main effect of face-half [F(1,95) = 76.2, p < .0001]: control subjects fixated the upper half longer. However, there was no interaction between phase and face-half.

Control results were highly similar if we narrowed the analysis to the eye and mouth regions specifically. ANOVA showed a main effect of phase [F(2,95) = 31.9, p < .0001]: Tukey's HSD test showed that controls spent more time looking in the learning phase than at targets or distractors in the recognition phase, and more time looking at distractors than targets in the recognition phase. There was a main effect of face part [F(1,95) = 83.5, p < .0001], with controls fixating the eyes longer, but no interaction between phase and face part.

For prosopagnosic subjects we first assessed total fixation duration on the whole face. During both the learning and the recognition phases, prosopagnosic subjects were comparable to the controls, the only exception being slightly longer fixation by B-IOT2 on distractors during the recognition phase.

Examining the upper/lower face index, control subjects spent about 20% longer looking at the upper face in all phases. Most prosopagnosic subjects behaved similarly, exceptions being B-IOT2 for targets and B-AT1 for distractors in the recognition phase, who both spent more time looking at the lower than the upper face (Fig. 6). Nevertheless the ANOVA showed an effect of group [F(2,26) = 9.82,

	Cont	rol	Occipitotemporal						Anterior temporal				
	Mean	SD	R-IOT1	R-IOT4	L-IOT2	B-IOT2	B-ATOT1	B-ATOT2	R-AT2	R-AT3	R-AT5	B-AT1	B-AT2
1 Change													
Eye position	96.73	5.55	89	100	39	89	72	28	89	100	33	94	100
Mouth position	98.50	2.71	100	94	72	100	100	100	100	100	94	100	100
Eye shape	99.50	1.73	100	100	72	100	78	89	100	100	78	100	100
Mouth shape	100.00	2.69	100	83	39	100	100	94	100	100	94	100	100
Forehead	99.50	1.73	100	100	94	100	100	100	100	100	89	94	100
Chin	99.50	1.73	100	100	100	100	89	100	100	100	89	100	100
2 Changes													
Eye position	99.00	2.34	78	78	11	83	39	22	100	94	39	89	100
Mouth position	99.03	2.26	100	89	78	94	100	83	100	100	78	83	100
Eye shape	99.08	3.18	94	100	72	78	50	67	100	94	72	89	94
Mouth shape	99.00	2.34	100	100	39	100	94	94	100	100	89	100	100
6 Changes													
Eye position	99.00	2.34	39	78	33	72	44	39	89	94	44	100	100
Mouth position	95.75	5.93	72	89	50	94	89	50	94	83	39	89	83
Eye shape	98.50	2.71	78	89	39	67	28	33	100	72	33	100	83
Mouth shape	94.87	6.83	61	94	67	94	56	22	78	94	44	83	94
Forehead	96.73	6.89	67	89	56	67	94	56	89	44	67	78	100
Chin	95.67	4.23	83	89	89	100	89	28	100	94	56	100	89
Bold text indicates impaired performance													

#### Table 3 - Results, Experiment 1.



Fig. 4 – Results, Experiment 1. Accuracy of patients is z-transformed in relation to the data of the control subjects, with scores for the upper face/eye region plotted on the x-axis and scores for the lower face/mouth region on the y-axis. Top row shows results for 1-change blocks, middle row for 2-changes blocks, and bottom row for 6-changes blocks. Points falling above the diagonal line would indicate more difficulty with upper face/eyes than the lower face/mouth. Dotted lines show the 95% limits for normal performance: points falling to the left of the vertical line indicate impairment for upper face/eye processing, while points falling below the horizontal line indicate impairment for lower face/mouth processing. Data for R-AT5 are flagged.

p < .0007] with Tukey's HSD test showing both anterior temporal and occipitotemporal groups having smaller upper/lower indices than controls, but not differing from each other. There was no effect of phase or interaction between group and phase.

Similarly, the eye/mouth index showed that controls spent 25% more time looking at the eyes than the mouth. Once more, most prosopagnosic subjects behaved similarly to the controls. The exceptions, with more time looking at the mouth than the eyes, were again B-IOT2, who demonstrated this for both targets and distractors in the recognition phase, and B-AT1, who showed this in the learning phase and for distractors in the recognition phase (Fig. 7). Again, the ANOVA showed an effect of group [F(2,26) = 10.2, p < .0005], with Tukey's HSD test showing both anterior temporal and occipitotemporal groups having lower eye/mouth indices than controls, but not differing from each other. There was no effect of phase or interaction between group and phase.

#### 4. Discussion

We found first that disproportionate impairment of perception of the eyes is most common among prosopagnosic subjects with occipitotemporal lesions. Second, the eyeprocessing impairment affected both configuration and feature shape, but not external contours. Third, while the eye/ mouth difference is more evident when subjects attend to multiple facial regions, it is still present when subjects attend to only one facial region or property. Finally, most prosopagnosic subjects still have the normal bias to fixate the eyes more, which makes less likely the explanation that they are simply not attending to the eyes.

Subjects with occipitotemporal lesions rather than those with anterior temporal lesions demonstrated greater impairments in processing the eye region. Could this be due to a greater prevalence of visual field defects? Studies of reading



Fig. 5 – Behavioral results, Experiment 2. A. Hits plotted against false alarms. Diagonal line indicates where hit rate would equal false alarm rate, indicating lack of discriminative power. B. d' (discriminative power) and c (criterion bias) are derived from the data in A. Prosopagnosic subjects show reduced discriminative power but similar criterion bias to controls.



Fig. 6 – Eye movement results, Experiment 2: upper versus lower face. Top graph shows data for the learning phase (A), bottom graphs for the retrieval phase, with previously seen targets on the left (B) and new distractor faces on the right (C). Points falling below the solid diagonal line indicate more time spent fixating on the upper than the lower face. For some stimuli B-IOT2 and B-AT1 show a tendency to scan the lower face more than the upper face.



Fig. 7 – Eye movement results, Experiment 2: eyes versus mouth. Top graph shows data for the learning phase (A), bottom graphs for the retrieval phase, with previously seen targets on the left (B) and new distractor faces on the right (C). Points falling below the solid diagonal line indicate more time spent fixating on the eye region than the mouth region. B-IOT2 and B-AT1 show for some stimuli a tendency to scan the mouth more than the eyes.

show that hemianopia can mimic effects attributed to disordered high-level visual processing (Bao, Rubino, Taylor, & Barton, 2015). However, of the six subjects, L-IOT2 and B-ATOT2 had intact visual fields, and the upper quadrantanopic defects of R-IOT4 and B-ATOT1 spared the central 5° and should not have affected the ability to see the face stimuli. B-IOT2 had bilateral constriction including a complete right hemianopia, but a previous study found that a control subject with complete hemianopia performed well at discriminating eye and mouth configuration when given unlimited time (Barton, 2008).

Most previous subjects with greater impairment of eye processing had similar lesions (Barton, 2008; Bukach et al., 2006, 2008; Busigny et al., 2010; Rossion et al., 2009). Of these, only PS had functional imaging, showing loss of the right occipital face area and left fusiform face area (Rossion et al., 2003). Functional imaging in our occipitotemporal cohort showed in common the loss of the right fusiform face area and often the occipital face area (Fig. 3). This complements a recent neuroimaging study in healthy subjects that showed that the fusiform face area is most sensitive to changes in the eyes (Lai et al., 2014).

The relative preservation of eye processing in prosopagnosic subjects with anterior temporal lesions may be simply consistent with the observation that these subjects have an associative than an apperceptive deficit (Barton, 2008; Liu, Pancaroglu, Hills, Duchaine, & Barton, 2014). Only R-AT5 showed perceptual deficits and an eve/mouth asymmetry comparable to those of subjects with occipitotemporal lesions. Of note, she had the most posterior extent of anterior temporal damage and the smallest volume of activation in her right fusiform face area. Nevertheless, some other subjects with anterior temporal lesions also showed milder eye processing deficits, especially with the difficult 6-changes condition. This underlines the fact that the apperceptive/ associative dichotomy is relative rather than absolute (Barton, 2008), and that more subtle perceptual deficits in face processing can be demonstrated in subjects with anterior temporal lesions (Barton, Zhao, & Keenan, 2003). Furthermore, our study does not address the possibility that subjects with anterior temporal lesions may show an eye/mouth asymmetry on a test probing facial memory rather than perception.

The eye-processing impairment in subjects with occipitotemporal lesions affected both configuration and feature shape. Likewise, prior reports found an eye-processing impairment for not only configural information but also various types of feature properties, including shape, brightness, and size (Bukach et al., 2006, 2008; Busigny et al., 2010; Ramon & Rossion, 2010; Rossion et al., 2009). The fact that both feature shape and configuration are similarly affected is consistent with previous assertions that configuration does not have a special status, but is merely one index of the complex three-dimensional shape of the face (Barton, 2008; Yovel & Duchaine, 2006). The lack of a difference for external contour indicates that the eye/mouth difference is specific to internal aspects of facial structure, at least for the full frontal views we used.

Greater impairment for processing the eyes was most evident under the difficult 6-changes condition. Because a change could occur in many different parts of the face, this condition stressed attention to the whole face. One might thus argue that greater impairment for eye processing may be related to holistic processing, as suggested by others (Caldara et al., 2005; Ramon & Rossion, 2010). However, deficits were still evident when attention could be focused on one facial region or even a single type of change. This would suggest that processing of the whole face is not necessary to reveal greater eye-processing impairment. Nevertheless, the part-whole paradigm shows that discriminating changes to a feature are easier when the feature is presented in a whole face than in isolation (Tanaka & Farah, 1993), and the composite face effect reveals that the perception of one half of the face is influenced by the other half (Young, Hellawell, & Hay, 1987): hence one cannot exclude some implicit whole-face effects in our regionally focused conditions. An alternative account of our findings would be simply that conditions with greater attentional demands are more likely to yield an eye/mouth asymmetry.

How subjects distribute attention across the face was the motivation for our eye movement study. The premotor theory of attention postulates a close link between attention and eye movements (Rizzolatti, Riggio, Dascola, & Umilta, 1987). While attention and fixation can be dissociated, as in covert attentional shifts while the eyes remain still, shifts in fixation are strongly linked to shifts of exogenous attention (Smith & Schenk, 2012). Consistent with previous studies (Henderson et al., 2005), we found that healthy subjects spent more time looking at the upper halves and the eyes when the task is to learn or recognize faces (Barton et al., 2006; Malcolm, Lanyon, Fugard, & Barton, 2008). These findings are also consistent with other evidence that healthy individuals base identity decisions on information from the upper face-half and eye region (Fisher & Cox, 1975; Shepherd et al., 1981; Vinette et al., 2004).

We asked whether our prosopagnosic subjects, particularly those with greater eye-processing impairments following right occipitotemporal damage, would fail to show a similar scanning bias for the eyes. If so, failure to attend to the eyes might underlie their poor performance with the eye region. The group analysis did find less emphasis on scanning the eyes over the mouth in subjects with occipitotemporal lesions. However, there are two observations that suggest this is not the explanation of their perceptual deficits. First, given the small size of our group, this effect may be driven by one outlier, subject B-IOT2. At an individual level, most occipitotemporal subjects showed a fixation distribution similar to controls. Second, a similar group effect was found for anterior temporal subjects, despite the fact that those subjects performed better on the perceptual tests.

Few previous studies have examined the fixations of prosopagnosic subjects viewing faces. Subject PS showed reduced scanning of the eyes (de Xivry et al., 2008), paralleling her reduced reliance on eyes for face identification (Caldara et al., 2005). However, subject 005A with a right occipitotemporal lesion showed normal emphasis on the eyes while subject 002D, who had childhood-onset prosopagnosia associated with polymicrogyria, did not (Barton et al., 2007). Patient SB, with bilateral occipitotemporal lesions, also had a normal emphasis of fixations on the eyes (Le et al., 2003). Thus, the data so far suggest that retained emphasis of fixations on the eyes is characteristic of most but not all patients with acquired prosopagnosia. Whether this difference reflects lesion extent, severity of the behavioral deficit, pre-morbid scanning preferences, individual coping strategy, or other factors is not clear.

Finally, it is of interest to compare these prosopagnosic results with those for the face inversion effect in healthy subjects. It has been proposed that since humans see faces mainly upright, their face expertise is orientationdependent. If so, performance of healthy subjects viewing inverted faces may parallel the performance of prosopagnosic subjects viewing upright faces, as in both situations expert face mechanisms may not be available. However, experiments with similar stimuli have shown that perception of the mouth is preferentially affected by inversion (Barton, Deepak, & Malik, 2003; J. J. Barton, Keenan, & Bass, 2001; Malcolm et al., 2004; Tanaka, Kaiser, Hagen, & Pierce, 2014). This has been attributed to the fact that when inversion makes long-range analysis over the entire face difficult, only processing of smaller facial regions is possible, and precedence is given to the most salient region, the eyes (Sekunova & Barton, 2008). Consistent with this, the inversion effect for mouth configuration is abolished when conditions are manipulated to shift attention to the mouth (Barton, Cherkasova, et al., 2001; Sekunova & Barton, 2008). In prosopagnosia, it is instead the processing of the highly salient eye region that is most degraded, and these eye processing deficits are improved but not eliminated by focused attention. These suggest two points. First, saliency and attention are important factors that determine the regional pattern of deficits in the face inversion effect. Second, in prosopagnosia due to occipitotemporal lesions, the normal eye advantage is lost. Since the fusiform face area shows activity that correlates with the normal hierarchy of facial features that emphasizes the eyes (Lai et al., 2014), the fact that this cortical region is preserved in healthy subjects viewing inverted faces but lost in our prosopagnosic subjects with occipitotemporal lesions may be relevant. Regardless, this underlines the limitations of using the face inversion effect to model prosopagnosia.

#### Acknowledgments

This work was supported by CIHR operating grant (MOP-102567) to JB. JB was supported by a Canada Research Chair and the Marianne Koerner Chair in Brain Diseases. BD was supported by grants from the Economic and Social Research Council (UK) (RES-062-23-2426) and the Hitchcock Foundation. We would like to thank all the patients and their families for their hard work and contributions.

#### Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.cortex.2016.04.024.

#### REFERENCES

- Bao, J. Y., Rubino, C., Taylor, A. J., & Barton, J. J. (2015). The effects of homonymous hemianopia in experimental studies of alexia. *Neuropsychologia*, 70, 156–164.
- Barton, J. (2003). Disorders of face perception and recognition. Neurologic Clinics, 21, 521–548.
- Barton, J. J. S. (2008). Structure and function in acquired prosopagnosia: lessons from a series of 10 patients with brain damage. *Journal of Neuropsychology*, 2(1), 197–225.
- Barton, J., & Cherkasova, M. (2003). Face imagery and its relation to perception and covert recognition in prosopagnosia. *Neurology*, 61, 220–225.
- Barton, J. J., Cherkasova, M. V., Hefter, R., Cox, T. A., O'Connor, M., & Manoach, D. S. (2004). Are patients with social developmental disorders prosopagnosic? Perceptual heterogeneity in the Asperger and socio-emotional processing disorders. Brain, 127(Pt 8), 1706–1716.
- Barton, J., Cherkasova, M., & O'Connor, M. (2001). Covert recognition in acquired and developmental prosopagnosia. *Neurology*, 57, 1161–1167.
- Barton, J. J., Deepak, S., & Malik, N. (2003). Attending to faces: change detection, familiarization, and inversion effects. *Perception*, 32(1), 15–28.
- Barton, J. J., Keenan, J. P., & Bass, T. (2001). Discrimination of spatial relations and features in faces: effects of inversion and viewing duration. British Journal of Psychology, 92(Pt 3), 527–549.
- Barton, J. J., Press, D. Z., Keenan, J. P., & O'Connor, M. (2002). Lesions of the fusiform face area impair perception of facial configuration in prosopagnosia. Neurology, 58(1), 71–78.
- Barton, J., Radcliffe, N., Cherkasova, M., & Edelman, J. (2007). Scan patterns during the processing of facial identity in prosopagnosia. Experimental Brain Research, 181(2), 199–211.
- Barton, J., Radcliffe, N., Cherkasova, M., Edelman, J., & Intriligator, J. (2006). Information processing during face recognition: the effects of familiarity, inversion and morphing on scanning fixations. Perception, 35(8), 1089–1105.
- Barton, J., Zhao, J., & Keenan, J. (2003). Perception of global facial geometry in the inversion effect and prosopagnosia. *Neuropsychologia*, 41, 1703–1711.
- Benton, A. L., & Van Allen, M. W. (1972). Prosopagnosia and facial discrimination. Journal of the Neurological Sciences, 15(2), 167–172.
- Bodamer, J. (1947). Die prosopagnosie. Archiv fur Psychiatrie und Nervenkrankheiten, 179, 6–54.
- Bruce, V., & Young, A. (1986). Understanding face recognition. British Journal of Psychology, 77, 305–327.
- Bukach, C. M., Bub, D. N., Gauthier, I., & Tarr, M. J. (2006). Perceptual expertise effects are not all or none: spatially limited perceptual expertise for faces in a case of prosopagnosia. Journal of Cognitive Neuroscience, 18(1), 48–63.
- Bukach, C. M., Le Grand, R., Kaiser, M. D., Bub, D. N., & Tanaka, J. W. (2008). Preservation of mouth region processing in two cases of prosopagnosia. *Journal of Neuropsychology*, 2(Pt 1), 227–244.
- Busigny, T., Joubert, S., Felician, O., Ceccaldi, M., & Rossion, B. (2010). Holistic perception of the individual face is specific and necessary: evidence from an extensive case study of acquired prosopagnosia. *Neuropsychologia*, 48(14), 4057–4092.

- Busigny, T., & Rossion, B. (2011). Holistic processing impairment can be restricted to faces in acquired prosopagnosia: evidence from the global/local Navon effect. *Journal of Neuropsychology*, 5(Pt 1), 1–14.
- Caldara, R., Schyns, P., Mayer, E., Smith, M., Gosselin, F., & Rossion, B. (2005). Does prosopagnosia take the eyes out of face representations? Evidence for a defect in representing diagnostic facial information following brain damage. *Journal* of *Cognitive Neuroscience*, 17(10), 1652–1666.
- Davies-Thompson, J., Pancaroglu, R., & Barton, J. (2014). Acquired prosopagnosia: structural basis and processing impairments. *Frontiers in Bioscience*, 6, 159–174.
- DeGutis, J., Cohan, S., Mercado, R. J., Wilmer, J., & Nakayama, K. (2012). Holistic processing of the mouth but not the eyes in developmental prosopagnosia. *Cognitive Neuropsychology*, 29(5–6), 419–446.
- Duchaine, B., Germine, L., & Nakayama, K. (2007). Family resemblance: ten family members with prosopagnosia and within-class object agnosia. *Cognitive Neuropsychology*, 24(4), 419–430.
- Duchaine, B., & Nakayama, K. (2006). The cambridge face memory test: results for neurologically intact individuals and an investigation of its validity using inverted face stimuli and prosopagnosic participants. *Neuropsychologia*, 44(4), 576–585.
- Ellis, H. D., & Florence, M. (1990). Bodamer's (1947) paper on prosopagnosia. *Cognitive Neuropsychology*, 7(2), 81–105.
- Fisher, G. H., & Cox, R. L. (1975). Recognizing human faces. Applied Ergonomics, 6(2), 104–109.
- Fox, C. J., Iaria, G., & Barton, J. J. S. (2009). Defining the face processing network: optimization of the functional localizer in fMRI. Human Brain Mapping, 30(5), 1637–1651.
- Gloning, I., Gloning, K., Hoff, H., & Tschabitscher, H. (1966). Zur Prosopagnosie. Neuropsychologia, 4, 113–132.
- Gloning, K., & Quatember, R. (1966). Methodischer beitrag zur Untersuchung der Prosopagnosie. Neuropsychologia, 4, 133–141.
- Henderson, J. M., Williams, C. C., & Falk, R. J. (2005). Eye movements are functional during face learning. Memory & Cognition, 33(1), 98–106.
- Hills, C. S., Pancaroglu, R., Duchaine, B., & Barton, J. J. (2015). Word and text processing in acquired prosopagnosia. Annals of Neurology, 78(2), 258–271.
- Joubert, S., Felician, O., Barbeau, E., Sontheimer, A., Barton, J. J., Ceccaldi, M., et al. (2003). Impaired configurational processing in a case of progressive prosopagnosia associated with predominant right temporal lobe atrophy. *Brain*, 126(Pt 11), 2537–2550.
- Kimchi, R., Behrmann, M., Avidan, G., & Amishav, R. (2012). Perceptual separability of featural and configural information in congenital prosopagnosia. *Cognitive Neuropsychology*, 29(5–6), 447–463.
- Klin, A., Jones, W., Schultz, R., Volkmar, F., & Cohen, D. (2002). Visual fixation patterns during viewing of naturalistic social situations as predictors of social competence in individuals with autism. Archives of General Psychiatry, 59(9), 809–816.
- Lai, J., Pancaroglu, R., Oruc, I., Barton, J. J., & Davies-Thompson, J. (2014). Neuroanatomic correlates of the feature-salience hierarchy in face processing: an fMRI – adaptation study. *Neuropsychologia*, 53, 274–283.
- Le, S., Raufaste, E., & Demonet, J. F. (2003). Processing of normal, inverted, and scrambled faces in a patient with prosopagnosia: behavioural and eye tracking data. Brain Research. Cognitive Brain Research, 17(1), 26–35.
- Levine, D., & Calvanio, R. (1989). Prosopagnosia: a defect in visual configural processing. Brain and Cognition, 10, 149–170.
- Liu, R. R., Pancaroglu, R., Hills, C. S., Duchaine, B., & Barton, J. J. (2014). Voice recognition in face-blind patients. *Cerebral Cortex*, 26(4), 1473–1487.

- Lundqvist, D., & Litton, J. E. (1998). The averaged Karolinska directed emotional faces—AKDEF.
- Malcolm, G. L., Lanyon, L. J., Fugard, A. J., & Barton, J. J. (2008). Scan patterns during the processing of facial expression versus identity: an exploration of task-driven and stimulusdriven effects. *Journal of Vision*, 8(8), 21–29.
- Malcolm, G., Leung, C., & Barton, J. (2004). Regional variation in the inversion effect for faces: different patterns for feature shape, spatial relations, and external contour. *Perception*, 33, 1221–1231.
- Pachai, M. V., Sekuler, A. B., & Bennett, P. J. (2013). Sensitivity to information conveyed by horizontal contours is correlated with face identification accuracy. Frontiers in Psychology, 4, 74.
- Peterson, M. F., & Eckstein, M. P. (2012). Looking just below the eyes is optimal across face recognition tasks. Proceedings of the National Academy of Sciences of the United States of America, 109(48), E3314–E3323.
- Ramon, M., & Rossion, B. (2010). Impaired processing of relative distances between features and of the eye region in acquired prosopagnosia-two sides of the same holistic coin? Cortex, 46(3), 374–389.
- Rickham, P. P. (1964). Human experimentation. Code of Ethics of the World Medical Association. Declaration of Helsinki. BMJ: British Medical Journal, 2(5402), 177.
- Rizzo, M., Hurtig, R., & Damasio, A. R. (1987). The role of scanpaths in facial recognition and learning. Annals of Neurology, 22(1), 41–45.
- Rizzolatti, G., Riggio, L., Dascola, I., & Umilta, C. (1987). Reorienting attention across the horizontal and vertical meridians: evidence in favor of a premotor theory of attention. *Neuropsychologia*, 25(1A), 31–40.
- Rossion, B., Caldara, R., Seghier, M., Schuller, A. M., Lazeyras, F., & Mayer, E. (2003). A network of occipito-temporal face-sensitive areas besides the right middle fusiform gyrus is necessary for normal face processing. Brain, 126(Pt 11), 2381–2395.
- Rossion, B., Kaiser, M. D., Bub, D., & Tanaka, J. W. (2009). Is the loss of diagnosticity of the eye region of the face a common aspect of acquired prosopagnosia? *Journal of Neuropsychology*, 3(Pt 1), 69–78.
- Sadr, J., Jarudi, I., & Sinha, P. (2003). The role of eyebrows in face recognition. Perception, 32(3), 285–293.
- Sekuler, A., Gaspar, C., Gold, J., & Bennett, P. (2004). Inversion leads to quantitative, not qualitative, changes in face processing. *Current Biology*: CB, 14, 391–396.
- Sekunova, A., & Barton, J. J. (2008). The effects of face inversion on the perception of long-range and local spatial relations in eye and mouth configuration. *Journal of Experimental Psychology*. *Human Perception and Performance*, 34(5), 1129–1135.

- Shepherd, J., Davies, G., & Ellis, H. (1981). Studies of cue saliency. In G. Davies, H. Ellis, & J. Shepherd (Eds.), Perceiving and remembering faces (pp. 105–131). London: Academic Press.
- Smith, D. T., & Schenk, T. (2012). The premolar theory of attention: time to move on? *Neuropsychologia*, 50(6), 1104–1114.
- Tanaka, J. W., & Farah, M. J. (1993). Parts and wholes in face recognition. Quarterly Journal of Experimental Psychology, 46(2), 225–245.
- Tanaka, J. W., Kaiser, M. D., Hagen, S., & Pierce, L. J. (2014). Losing face: impaired discrimination of featural and configural information in the mouth region of an inverted face. Attention, *Perception & Psychophysics*, 76(4), 1000–1014.
- Van Belle, G., Busigny, T., Lefevre, P., Joubert, S., Felician, O., Gentile, F., et al. (2011). Impairment of holistic face perception following right occipito-temporal damage in prosopagnosia: converging evidence from gaze-contingency. *Neuropsychologia*, 49(11), 3145–3150.
- Van Belle, G., De Graef, P., Verfaillie, K., Busigny, T., & Rossion, B. (2010). Whole not hole: expert face recognition requires holistic perception. *Neuropsychologia*, 48(9), 2620–2629.
- Vinette, C., Gosselin, F., & Schyns, P. G. (2004). Spatio-temporal dynamics of face recognition in a flash: it's in the eyes. *Cognitive Science*, 28(2), 289–301.
- Warrington, E. K. (1984). Recognition memory test. Windsor: NFER-NELSON.
- Weiner, K. S., Golarai, G., Caspers, J., Chuapoco, M. R., Mohlberg, H., Zilles, K., et al. (2014). The mid-fusiform sulcus: a landmark identifying both cytoarchitectonic and functional divisions of human ventral temporal cortex. *NeuroImage*, 84, 453–465.
- de Xivry, J.-J. O., Ramon, M., Lefèvre, P., & Rossion, B. (2008). Reduced fixation on the upper area of personally familiar faces following acquired prosopagnosia. *Journal of Neuropsychology*, 2(1), 245–268.
- Yi, L., Fan, Y., Quinn, P. C., Feng, C., Huang, D., Li, J., et al. (2013). Abnormality in face scanning by children with autism spectrum disorder is limited to the eye region: evidence from multi-method analyses of eye tracking data. *Journal of Visualization*, 13(10).
- Young, A. W., Hellawell, D., & Hay, D. C. (1987). Configurational information in face perception. *Perception*, 16(6), 747–759.
- Yovel, G., & Duchaine, B. (2006). Specialized face perception mechanisms extract both part and spacing information: evidence from developmental prosopagnosia. *Journal of Cognitive Neuroscience*, 18(4), 580–593.