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Reduced fixation on the upper area of personally familiar faces following acquired prosopagnosia

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Selective impairment of face recognition following brain damage, as in acquired prosopagnosia, may cause a dramatic loss of diagnosticity of the eye area of the face and an increased reliance on the mouth for identification (Caldara *et al.*, 2005). To clarify the nature of this phenomenon, we measured eye fixation patterns in a case of pure prosopagnosia (PS, Rossion *et al.*, 2003) during her identification of photographs of personally familiar faces (27 children of her kindergarten). Her age-matched colleague served as a control. Consistent with previous evidence, the normal control identified the faces within two fixations located just below the eyes (central upper nose). This pattern (location and duration) of fixations remained unchanged even by increasing difficulty by presenting anti-caricatures of the faces. In contrast, the great majority of the patient's fixations, irrespective of her accuracy, were located on the mouth. Overall, these observations confirm the abnormally reduced processing of the upper area of the face in acquired prosopagnosia. Most importantly, the prosopagnosic patient also fixated the area of the eyes spontaneously in between the first and last fixation, ruling out alternative accounts of her behaviour such as, for example, avoidance or failure to orient attention to the eyes, as observed in autistic or bilateral amygdala patients. Rather, they reinforce our proposal of a high-level perceptual account (Caldara *et al.*, 2005), according to which acquired prosopagnosic patients have lost the ability to represent multiple elements of an individual face as a perceptual unit (holistic face perception). To identify a given face, they focus very precisely on local features rather than seeing the whole of a face from its diagnostic centre (i.e. just below the eyes). The upper area of the face is particularly less attended to and less relevant for the prosopagnosic patient because it contains multiple features that require normal holistic perception in order to be the most diagnostic region. Consequently, prosopagnosic patients develop a more robust representation of the mouth, a relatively isolated feature in the face that may contain more information than any single element of the upper face area, and is thus sampled repeatedly for resolving ambiguity in the process of identification.

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There is considerable evidence that the region of the eyes is dominant for face identification. Human adults can recognize and remember faces only from the eyes (McKelvie, 1976). Experiments designed to measure the relative importance of different internal facial features for individual face recognition have consistently shown the dominance of the eye/eyebrow combination, followed by the mouth and then the nose (Davies, Ellis, & Shepherd, 1977; Fraser, Craig, & Parker, 1990; Haig, 1985; Sergent, 1984; Tanaka & Farah, 1993; Walker-Smith, Gale, & Findlay, 1977). Response classification methods revealing partial information during face recognition also largely support the dominant role of the eye area for correct face identification (Gosselin & Schyns, 2001; Haig, 1985, 1986; Sekuler, Gaspar, Gold, & Bennett, 2004), and there is even evidence that the eyebrows alone convey critical information to recognize faces (Haig, 1986; Sadr, Jarudi, & Sinha, 2003).

The predominant role of the area around the eyes for recognition characterizes the normal adult face processing system (see also, e.g. Taylor, Edmonds, McCarthy, & Allison, 2001 for developmental evidence of the importance of processing of the eyes). However, there is recent evidence that brain-damaged patients who are impaired at recognizing faces – prosopagnosia (Bodamer, 1947; Quaglino & Borelli, 1867; Sergent & Signoret, 1992) – rely on the area of the eyes to a far lesser degree when compared with normal controls, even when provided with sufficient time and information for correct identification. This was observed by Caldara and colleagues (2005) who tested a single case of prosopagnosia with preserved object recognition (PS, Rossion *et al.*, 2003) by means of a response classification method revealing facial information randomly across spatial locations of the face ('Bubbles', Gosselin & Schyns, 2001; for the origin of the method, see Haig, 1985, 1986). In this study, the patient PS had to learn 10 photographs of individual faces that she subsequently had to identify over thousands of trials. On every single trial, the face photograph was revealed through a number of apertures ('Bubbles') randomly located on the face image. The patient's performance was maintained at 75% by increasing or decreasing the number of Bubbles throughout the experiment, collecting images corresponding to correct and incorrect responses (Gosselin & Schyns, 2001). Unsurprisingly, the prosopagnosic patient did not only learn the faces more slowly, but also required a much larger amount of Bubbles (i.e. information) to perform the task at the same level as normal participants. More interestingly, response classification images, contrasting correct and incorrect trials, showed that the patient did not use information located on the eye area at all, relying almost exclusively on the lower part of the face for correct face identification (mouth and lower external contours; see Caldara *et al.*, 2005). In contrast, normal participants relied primarily on the eye area of the face, with a preference for the right eye (i.e. left visual field; see also Gosselin & Schyns, 2001). This reduced diagnosticity of the eyes, which has also been observed in two other cases of acquired prosopagnosia without object recognition impairments (Bukach, Bub, Gauthier, & Tarr, 2006; Bukach, Le Grand, Kaiser, Bub, & Tanaka, 2008, this issue). While these patients were dramatically impaired at matching pictures of unfamiliar faces differing by the eyes, they performed equally or even better than normal participants when the mouth was diagnostic for individual discrimination.

These observations are important because they suggest that acquired prosopagnosia is a *qualitative* deficit of face processing: distinct facial cues/processes are affected to a different extent. The study of prosopagnosia thus potentially provides some information about the nature of normal face perception.

However, an important and unresolved question is whether these observations reflect mainly a lack of spontaneous attention of the patient to the eyes of faces (i.e. avoidance), or a real inability to extract diagnostic information particularly from this area, which in-turn promotes increased reliance on the mouth. In the former scenario, the prosopagnosic patient, as a result of his/her deficit in face recognition, would simply pay less attention to the eyes of others' faces, perhaps to avoid social discomfort (i.e. 'staring'), and thus would not even attempt to use this information to recognize other people. Alternatively, the patient could still look at and pay attention to the eyes of other's faces, but the information derived from this area being no longer (or less) diagnostic for identification, the patient would rather concentrate on other areas of the face, such as the mouth.

This issue needs to be resolved because there is evidence that other pathological populations showing face processing impairments, such as autistic children (for a recent review see Jemel, Mottron, & Dawson, 2006), also rely less on the eyes of faces. For instance, children with autism spend less time fixating the eyes of faces (Klin, Jones, Schultz, Volkmar, & Cohen, 2002; Pelphrey *et al.*, 2002; but see Spezio, Adolphs, Hurley, & Piven, 2007a; Van der Geest, Kemner, Camfferman, Verbaten, & van Engeland, 2002) with the amount of time devoted to this region being correlated with autism (Klin *et al.*, 2002). These patients also show increased fixation duration on the mouth (Klin *et al.*, 2002; Spezio *et al.*, 2007a), and 'Bubbles' reveals their greater reliance on the mouth and decreased use of the eyes during facial expression judgments (Spezio *et al.*, 2007a). Thus, in the case of autism, there is an avoidance of eye-contact and less reliance on the eyes, presumably due to a social interaction deficit. Similarly, bilateral amygdala damage may cause an inability to make normal use of information from the eye region for facial expression judgments (Adolphs *et al.*, 2005). This appears to be due to a lack of spontaneous fixations on the eyes during free viewing of faces rather than an inability to extract diagnostic information from this area (Adolphs *et al.*, 2005; Spezio, Huang, Castelli, & Adolphs, 2007b). Thus, at first glance, large, a reduced reliance on the eyes appears to be a common aspect of multiple face processing deficits, but the underlying causes and mechanisms of these neurofunctional impairments are likely to be different and demand clarification.

Another unresolved issue is whether the increased reliance on the mouth at the expense of the eye area of the face extends to the recognition of full face stimuli, i.e. when all facial cues are presented simultaneously. Indeed, for all their interest, one limitation of methods such as 'Bubbles' is that they reveal only partial information on each trial (e.g. through apertures in Endo, 1986; Gosselin & Schyns, 2001; Haig, 1985, 1986; or through noise-free areas such as in Sekuler *et al.*, 2004), a factor which possibly disrupts normal face processes as observed with full face stimuli (Endo, 1986; Goffaux & Rossion, 2006). As for the evidence collected with unfamiliar face pictures in matching tasks, it is done with highly similar stimuli that vary in terms of single features or abnormal distances between features (Bukach *et al.*, 2006, 2008). Thus, the information attended to and utilized by acquired prosopagnosic patients during identification of full pictures of familiar faces, i.e. with all features simultaneously available, remains to be determined.

In the present study, we aimed at clarifying these questions, overcoming these limitations, and more generally extending the findings of Caldara *et al.* (2005) regarding this abnormal balance of eye/mouth diagnosticity observed with the brain-damaged prosopagnosic patient PS. To do so, we recorded the eye fixations of PS during identification of personally familiar faces. This patient is particularly interesting, not only because her deficit is restricted to the category of faces and her pattern of occipitotemporal lesions sparing the right middle fusiform gyrus ('fusiform face area', 'FFA'; see Rossion *et al.*, 2003; Sorger, Goebel, Schiltz, & Rossion, 2007), but also due to her excellent memory and ability to perform complex tasks for long durations, as well as her active social and professional life. In particular, we took advantage of the fact that, despite her prosopagnosia, the patient is still working as a kindergarten teacher. Over the course of the entire year (3 days per week) she supervises a group of about 25 children (3–4 years of age), which changes annually. Even though she reports a few anecdotes of misidentification, PS deals extremely well with the situation of having to efficiently discriminate and recognize the individual children (half of the group at a time, either in the morning or the afternoon) in the limited classroom environment. To do so, she admits requiring a high degree of concentration, and claims to rely on multiple cues besides faces, such as the voice, the gait, the height of the children, the hair colour, etc . . . Yet, when the set of stimuli is not mixed with unfamiliar faces, her recognition from static full photographs of the children is very good, and still well above chance level for cropped faces revealing only internal features (Ramon & Rossion, 2007). Here we used this opportunity to characterize PS's fixation patterns during an identification task using the set of highly familiar and homogenous faces of her kindergarten pupils, which is ideal for several reasons. First, the patient's degree of familiarity with the faces is both quantitatively and qualitatively much more important than with learned photographs of unfamiliar faces or famous faces because she is repeatedly and extensively exposed to these children faces in real life, under various viewing conditions. Second, the patient's amount of exposure and degree of familiarity with the different faces is roughly equal, unlike the tests that are done with famous face photographs for instance. Third, the set of faces is quite homogenous, with children of that age having less or no individual cues that characterize adults' faces (e.g. make-up, piercing, spots, pilosity . . .) and could influence recognition performance. Fourth, despite her prosopagnosia, the patient can identify these faces much better than at chance, but still makes a large proportion of mistakes, allowing a comparison of eye fixation patterns for correct and incorrect responses. Finally, whereas a normal participant is expected to recognize personally familiar faces within the first fixation(s), the prosopagnosic patient PS usually takes several seconds to name a face (Ramon & Rossion, 2007), thus presumably engaging in multiple saccades and long fixation durations before providing a response, which in-turn permits a detailed characterization of eye fixation patterns during identification of personally familiar faces.

To summarize, we hypothesized that the prosopagnosic patient PS would show a reduced amount of time and number of fixations within the area around the eyes, accompanied by a predominance of the mouth region, consistent with our results in the response classification experiment (Caldara *et al.*, 2005). This pattern of fixations during face identification should prove to be abnormal as compared to the normal control tested here (PS's only age-matched colleague), who was expected to fixate the eyes or the nose more than the mouth, as is usually observed for normal viewers during face encoding and recognition (e.g. Althoff & Cohen, 1999; Barton, Radcliffe, Cherkasova, Edelman, & Intriligator, 2006; Henderson, Falk, Minut, Dyer, & Mahadevan, 2001). Yet, given the patient PS's personal reports, and contrary to observations in autistic or bilateral amygdala damaged patients, we also expected to find a substantial amount of spontaneous attention to the eyes for PS. Finally, we hoped to reveal differences between PS's eye-movement patterns throughout the duration of stimulus presentation, and between correct and incorrect trials that would allow us to gain further information about the functional deficit underlying acquired prosopagnosia.

Methods

Participants

The patient PS has been tested and described extensively in previous publications (Caldara *et al.*, 2005; Mayer & Rossion, 2007; Rossion *et al.*, 2003; Schiltz *et al.*, 2006; Sorger *et al.*, 2007) and her case will only be summarized here. PS was born in 1950 and sustained closed head injury in 1992 that left her with major lesions of the left mid-ventral (mainly fusiform gyrus) and the right inferior occipital cortex. Minor damages to the left posterior cerebellum and the right middle temporal gyrus were also detected (see Sorger *et al.*, 2007). After medical treatment and neuropsychological rehabilitation, PS recovered extremely well from her cognitive deficits following the accident (Mayer & Rossion, 2007). Her only continuing complaint remains a profound difficulty in recognizing familiar faces, including those of her family when they are presented out of context. To determine a person's identity, she relies not only on external (non-face-inherent) cues such as haircut, moustache, or glasses, but also on the person's voice, posture, gait, etc. She may also use sub-optimal facial cues such as the mouth or the external contour of the face to recognize people, and is particularly impaired at extracting diagnostic information from the eyes of the face, as described in the introduction (Caldara *et al.*, 2005). Effectively, PS is like normal participants (100%, fast) to discriminate faces from other objects but is impaired and slowed down at recognizing faces at the individual level (Schiltz *et al.*, 2006). The Benton Face Recognition Test (BFRT) (Benton & Van Allen, 1968) ranks her as highly impaired, and her score at the Warrington Recognition Memory Test (WRMT) for faces characterizes her as significantly less accurate than controls [see Table 1 in (Rossion *et al.*, 2003)]. PS does not present any difficulty in recognizing objects, even at the subordinate level (Rossion *et al.*, 2003; Schiltz *et al.*, 2006). Her visual field is almost full (small left paracentral scotoma) and her visual acuity is good (0.8 for both eyes as tested in August 2003). In the present study, the patient PS was compared to the only control that we could test, her age-matched colleague in the kindergarten (YG, 60 years old, right-handed) who is also extremely familiar with the children faces used in the study. Both of them were tested after 10 months of visual experience with the faces, but for practical reasons the normal control was tested a few months later than PS. Similarly to PS, she was presented with a refresher test of the children faces before the eye fixation experiment, and she identified all the faces without any difficulty.

Stimuli

High-quality full-front photographs of the 27 children (10 females) of the kindergarten, well known by the patient, were used in the experiment. They had a neutral expression, mouth closed and eyes opened, and were cropped of external features (Figure 1). They were realigned on the pupils and presented in 256 colours. They spanned about $12 \times 16^\circ$ of visual angle (30×42 cm on the screen).

To increase task difficulty and number of fixations for the control participant so as to have another form of comparison with the patient PS, we also created anti-caricatures (e.g. Rhodes, Brennan, & Carey, 1987) of the 16 female faces using the following procedure (see e.g. Levin, 2000). Pairs of faces were morphed (Morph TM) iteratively to create an average face stimulus of the 16 faces. Eight pairs were generated, the 50% morph stimuli (50% position, hue and luminance between the two base images) of which were extracted from these morph continua, and then morphed further by pairs to obtain a final average face of the 16 individual faces (i.e. 8, 4, 2, and 1 final average face).

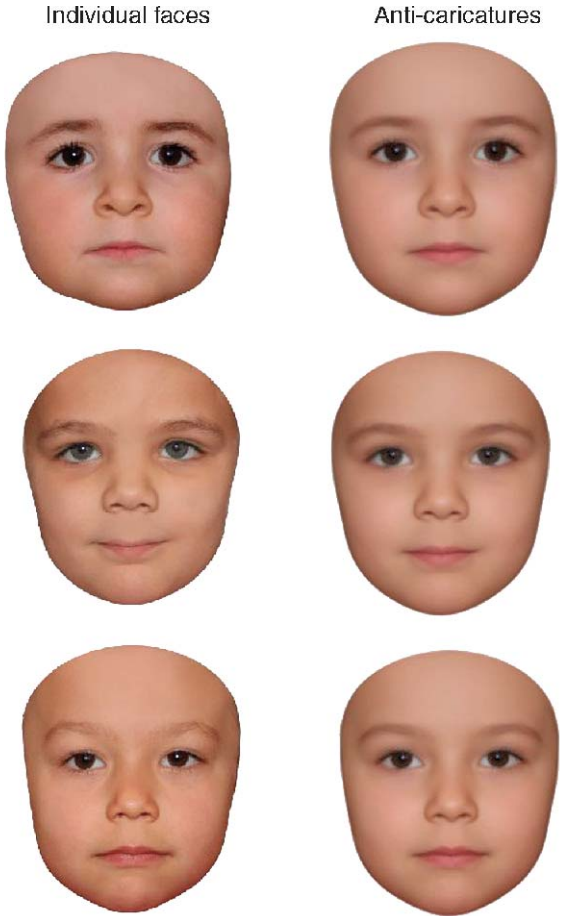

Figure 1. Examples of face stimuli used in the eye fixation experiment as well as the anti-caricatures (30% of the veridical face; 70% of the average face of 16 children faces) of these faces.

For all morphs, 100 points were matched between each image on analogous facial regions (i.e. centre of pupils, tip of the nose). Then, each original face stimulus was morphed with the average face, to extract face stimuli that had only 30% of their idiosyncratic features (70% of the average face, see Figure 1) and were thus much harder to recognize.

Procedure

The participants sat in a dimly lit room in front of a wide projection screen on which the images of the children's faces were displayed one by one. They were told to be as accurate as possible and had maximally 60 seconds to identify a child's face by providing its name, upon which the experimenter interrupted the trial by pressing a button. Subsequently, another child's photograph was selected randomly from the pool of 27, and the next trial was started automatically. If PS failed to identify the child's face within 60 seconds, the next trial was initiated. The trials were presented in blocks of 30 trials, which always began with a fixation dot presented at the centre of the picture during 1 second (see Figure 2). The patient performed 15 blocks of 30 trials in four sessions

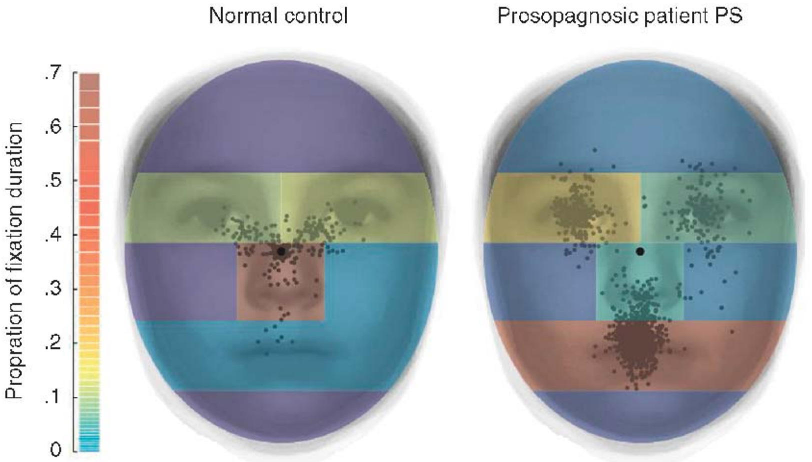

Figure 2. Representation of the different scoring regions superimposed on the average picture from all children. The colour of each scoring region corresponds to the proportion of fixation duration yielded by the colour bar on the left of the panel. The large Black dot corresponds to the fixation point displayed just before the picture. Only successful trials were selected. Each small Black dot represents one fixation. (A) Control participant and (B) the prosopagnosic patient PS. Besides the large amount of fixations on the mouth, note that PS's fixations fall exactly on the centre of each feature, in contrast to the normal participant's fixations, localized centrally, below the eyes.

(450 trials). Out of the valid 353 trials (no blinks, good pupil detection), we obtained a total of 212 trials with correct response for analysis (61% accuracy). The control participant performed 344 trials, with 191 valid trials for normal (veridical) faces, all correct (100% accuracy). For anti-caricatures, she performed 330 trials, with 170 valid trials, and 147 trials with a correct response. At the beginning of each block, a calibration procedure was performed.

We recorded PS's and the control participant's eye-movements at 200 Hz using a Chronos eye tracker (Skalar Medical BV, The Netherlands) while her head was restrained by a chin rest. The pictures were projected on a flat white screen (2×1.5 m) that was 1.5 m distant from the participants. The projector (Barco Cine8) was controlled by a VSG5/2 (Cambridge Research System Ltd, UK) running script written in Matlab (Mathworks, Natic, MA). Eye and target data were stored on a PC for off-line analysis. Fixation period at the start of each trial was used to realign eye and target before the scanning of the face. Eye position was filtered at 35 Hz using zero-phase digital filter (auto-regressive forward–backward filter) and velocity and acceleration signals were derived from position signals using a central difference algorithm on a $\pm$ 10 ms interval. Fixations were detected using a 5 deg/s velocity threshold. Periods during which the vectorial eye velocity was lower than the threshold during a minimum of 200 ms and which started at least 100 ms after the extinction of the fixation point were selected. The horizontal and vertical components of eye position were computed as the average values over the whole fixation interval. Depending on its average horizontal and vertical position, each fixation was assigned to a particular scoring region as defined by Henderson *et al.* (2001). These regions of interest for analysis contained one specific feature of the face (forehead, left eye, right eye, nose, left cheek, right cheek, mouth, and chin; see Figure 2). Then, for each scoring region, we computed the proportion of fixation duration (PFD), which represents the percentage of time that the patient spent fixating on a scoring region. For each child, we first summed the fixation durations on each scoring region and then normalized this result by the time that the participant spent scanning this child picture (the sum of the durations of all fixations). The inter-child mean PFD was then obtained by averaging the PFD across all children. Similarly, the proportion of the number of fixations was obtained by computing the proportion of the number of fixations falling within a particular scoring region. One child was never correctly identified by PS and thus all analyses were performed on the data for 26 children (also for the control). Proportions of fixation duration and number of fixations (dependent variables) were averaged for each child for the data analysis, and entered into Analyses of Variance (ANOVAS) with the between-factor participant (PS vs. control) and within-factor *face region* (mouth, right eye, left eye, and nose). Since there were very few fixations on the other areas of the face than the two eyes, mouth and nose for both PS ($<3.1\%$) and the control ($<2.7\%$), these last four areas only were considered in the analysis. Note that the dependent variables being proportions of durations and number of fixations, we did not expect any main effect of the factor *participant*, but hypothesized to disclose significant interactions between *participant* and *face region* fixated. In addition, since PS made quite a number of misidentifications and a large number of fixations, we also ran repeated ANOVAs on her data with *face region*, *rank* (first, second, second to last, or last fixation), and *correctness* of the response (correct or incorrect). Degrees of freedom were adjusted using Greenhouse–Geisser's procedure.

Results

Behavioural results and number of fixations

Overall, PS identified the children in 61% of the trials (chance level: $1/27 = 3.7\%$), her mean response time was 12.5 seconds. Her average number of fixations per face was 6.68 (± 0.45 *SE*). In contrast, the normal control did not make a single mistake and her mean response time was 1.86 seconds. She identified all of the faces in less than two fixations (mean: 1.80 ± 0.13 *SE*). On average, the duration of a single fixation was longer for PS (452 ± 3.8 ms *SE*) than the control participant (318 ± 6 ms *SE*) ($p < .001$).

Fixation durations on the different areas of the faces

Most interestingly, the pattern of fixations for face identification was completely different for the two participants. The control participant fixated the upper part of the nose longer than any other area (67%), followed by the eyes (28% in total) and the mouth (2%) (Figures 2 and 3A). In contrast, PS spent the majority of the time fixating on the mouth region (61% of fixation duration) of the face (Figures 2 and 3B). However, she also focused on the eyes for 29% of the fixation duration. She spent 6% of fixation duration on the nose area.

The ANOVA for repeated measures with participants (2) and areas (4) as factors showed a highly significant interaction between the two factors ($F_{2.39,\,119.86} = 264.11$, $p < .0001$). Planned comparisons (bonferroni corrected) showed that PS fixated the mouth longer than the control participant ($p < .0001$) and the nose less ($p < .0001$). The right eye was fixated longer by PS than the control ($p = .049$), and the opposite difference was found for the left eye ($p = .026$). In total, there was no significant difference in terms of the duration of fixation on the eye area (averaged over the two eyes) between PS and the control participant (paired t test, $t_{25} = 0.26$, $p = .8$), even

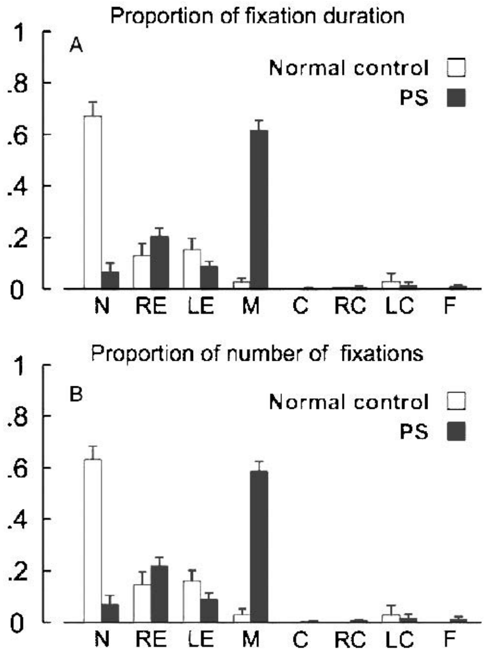

Figure 3. (A) Histogram of the inter-child mean (± 0.95 confidence interval) proportion of fixation duration for each scoring region for the control participant and PS. (B) Histogram of the inter-child mean (± 0.95 confidence interval) proportion of the number of fixations for each scoring region for the control participant and PS. RE: Right Eye; LE: Left Eye; N: Nose; M: Mouth; C: Chin; RC: Right Cheek; LC: Left Cheek; F: Forehead.

though it is worth noting that while the control's fixations were located mostly below the eyes and close to the centre of the face, PS's fixations fell exactly on the eyeballs (Figure 2). Hence, even at this level, PS and the normal control appear to show a different fixation pattern (see below). Considering the data intra-individually, PS showed longer fixations for the mouth when compared with any other area (all ps $< .0001$) and for the right eye compared to the left eye ($p < .001$), as well as for either of the two eyes as compared to the nose (ps $< .01$). The control participant fixated the nose longer than any other area (ps $< .0001$), followed by the eyes (no difference between left and right eye, $p = .37$), which were fixated longer than the mouth (ps $< .01$).

Number of fixations on the different areas of the faces

Confirming the fixation duration measures, 63% of the control participants' fixations were located within the nose area whereas 31% covered the eyes in total and merely about 3% positioned on the mouth. In contrast, the importance of the mouth for PS was confirmed by the proportion of the number of fixations falling within that particular region (59%, Figure 3B), with 30% fixations on the eyes in total and 7% on the nose.

The results of the statistical comparisons for the number of fixations were virtually identical to the durations of fixation. The ANOVA for repeated measures with participants (2) and areas (4) as factors showed a highly significant interaction between the two factors ($F_{2.59, 129.72} = 225.21, p < .0001$). Planned comparisons (bonferroni corrected) showed that PS fixated the mouth longer than the control participant ($p < .0001$) and the nose less ($p < .0001$). The right eye was not fixated more by PS than the control ($p = .08$) but the control participant had more fixations on the left eye than PS ($p < .05$). In total, there was no significant difference in terms of the amount of fixation on the eye area (averaged over the two eyes) between PS and the control participant (paired t test, $t_{25} = 0.028$, $p = .97$). Considering within-paticipant data analysis, PS showed a larger amount of fixations for the mouth when compared with all other areas (all ps $< .0001$) and for the right compared to the left eye ($p < .001$), as well as for either of the two eyes as compared to the nose (ps $< .01$). The control participant fixated the nose more than any other area (ps $< .0001$) followed by the eyes (no difference between left and right eye, $p = .61$), which were fixated more than the mouth (ps $< .01$).

Control's scanning of anti-caricatures as compared to PS's fixation pattern

When identifying anti-caricatures of the children's faces, the control participant scored 86% and took 7.24 seconds to answer. This provided a large number of fixations (9.49 fixations/face on average), thus more comparable to PS's pattern with normal pictures, at least quantitatively. However, on average, fixation duration was still longer for the patient PS (452 ± 3.8 ms *SE*) presented with normal faces than the control participant presented with anti-caricatures (349 ± 4 ms *SE*) ($p < .001$).

Despite the increase in difficulty and time taken to identify the anti-caricatures, the control participant's fixation pattern was still in total contrast with PS's dominant focus on the mouth. In fact, all fixations were located on the upper area of the face (Figure 4A), slightly above her fixations for the veridical faces (compare Figures 2–4A). This slight shift towards the upper area of the face led to a reversal of the proportions of fixation durations between the eyes and nose: 64% of the fixation durations were associated with the eyes, 32% with the nose in total, and about 4% with the mouth (Figure 4B).

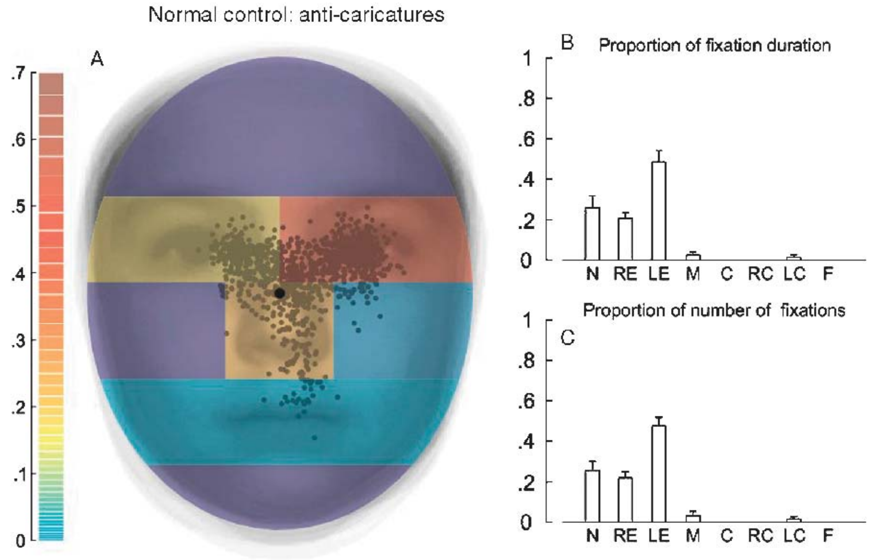

Figure 4. (A–C) Localization of fixations for the normal control participant tested with anti-caricature faces. The difficulty of identification and number of fixations was increased, which did not result in an increase in fixations on the mouth, but instead in a larger amount of fixations on the upper area of the face, the eyes in particular (compare to Figure 2).

The ANOVA for repeated measures of fixation duration with *participants* (2) and *areas* (4) as factors showed a highly significant interaction between the two factors ($F_{2.08, 62.68} = 161.62, p < .0001$). Planned comparisons (bonferroni corrected) showed that PS fixated the mouth longer than the control participant ($p < .0001$) and the nose for a shorter duration ($p < .0001$). The right eye was not fixated longer by PS than the control ($p = .37$) but the control participant showed more fixations located on the left eye than PS ($p < .0001$). In total, the control participant fixated the eye area much longer than PS (paired t test, $t_{15} = 11.3$, $p < .0001$). Within-participant analyses revealed that PS fixated the mouth longer than any other area (all ps $< .0001$), the same holds for the right compared to the left eye ($p < .001$), as well as for either of the two eyes as compared to the nose (ps $< .01$). The control participant fixated the left eye longer than any other area (ps $< .0001$) followed by the right eye and the nose (no difference: $p = .68$), which were fixated longer than the mouth (ps $< .01$).

The analysis for the number of fixations provided a similar outcome (Figure 4C) with a highly significant interaction between the two factors *participants* and *areas* ($F_{2.08, 62.68} = 164.52, p < .0001$). Planned comparisons (bonferroni corrected) showed that PS fixated the mouth more than the control participant ($p < .0001$) and the nose less ($p < .0001$). The right eye was not fixated more by PS than the control ($p = .56$), but the control participant had more fixations on the left eye than PS ($p < .0001$). In total, the control participant fixated the eye area of the face much more than PS (simple t test, $t_{15} = 12.36$, $p < .0001$). Considering data within participant, PS showed more fixations for the mouth than any other area (all ps $< .0001$) and for the right as opposed to the left eye ($p < .001$), as well as for either of the two eyes as compared to the nose (ps $< .01$). The control participant fixated the left eye more than any other area (ps $< .0001$) followed by the right eye and the nose (no difference: $p = .29$), which were both fixated more than the mouth (ps $< .01$).

Time course of fixations for the prosopagnosic patient PS

While the control participant identified the veridical faces within two fixations, and her fixations were all localized on the same region (centrally, upper part of the nose for veridical faces, just below the eyes for anti-caricatures), PS's locations of fixations were more distant from each other, as the patient focused on both the mouth and the eyes. To clarify this pattern in more detail, we ran a complementary analysis on PS's data, taking into account the time course of fixations during the face identification task (Figure 5). Proportion of fixation duration was entered in a two-way ANOVA with 4 (*areas*) × 4 (*fixation rank*) factors. There were main effects of the area fixated ($F_{1.9, 47.65} = 121.67$, $p < .0001$) and of the successive fixations ($F_{1.93, 48.3} = 4.31$, $p < .01$). Most interestingly, there was an interaction between the two factors, such that the distribution of fixation changed over the time course of the identification ($F_{9, 225} = 13.13, p < .0001$). Separate ANOVAs for each stage of fixation showed that for the first fixation, there was a large effect of face area ($F_{1.08, 27.07} = 267.9, p < .0001$). The first fixations were located almost exclusively within the mouth region (88% when compared with all other regions: ps $< .0001$) with a few on the nose (10%) fixated more than either of the two eye areas (ps $< .01$), which did not differ significantly from each other (less than 1%, Figure 5). The second fixation ($F_{1.32, 32.98} = 24.42, p < .0001$) was still mainly centred on the mouth region (59%, vs. all other areas: $p < .0001$) but the importance of the other regions increased. The right eye was fixated more than all other face areas (27%, ps $< .005$), with a significant difference with the left eye (8%, $p < .01$)

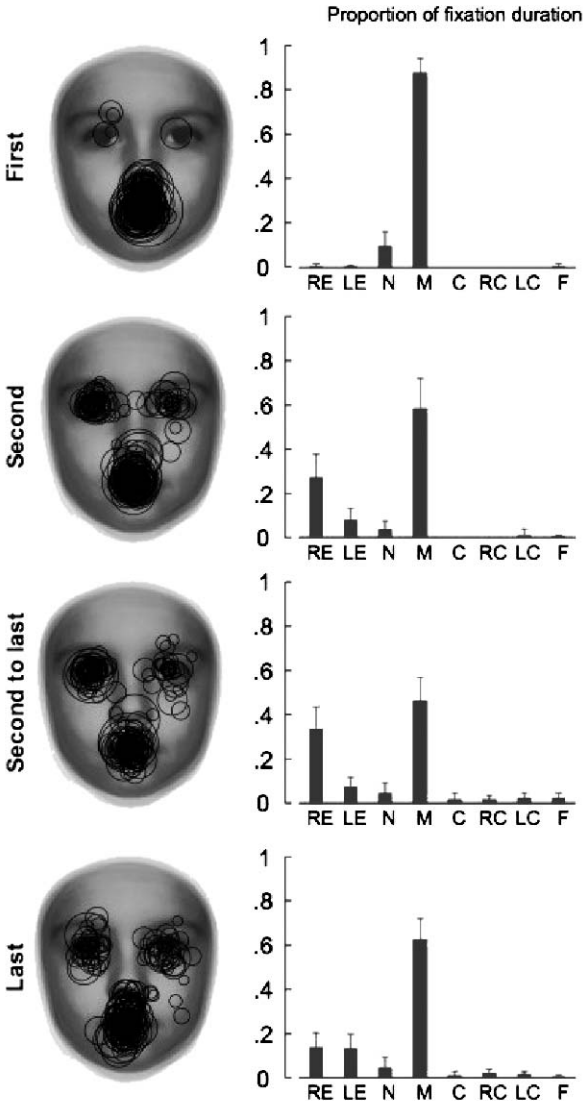

Figure 5. Left column: Representation of the first, second, second to last and last fixations on the average picture from all children. The diameter of the circle is proportional to the duration of the fixation. It is centred on the position of the fixation. Right column: Histogram of the inter-child mean (± 0.95 confidence interval) proportion of fixation duration on each scoring region. Only successful trials were selected.

and the nose (4%, $p < .001$), which did not differ significantly ($p > .24$). This pattern was further increased for the second to the last fixation ($F_{1.74,\,43.4} = 21.42, p < .0001$), with 46% of fixations located within the mouth area and comparably on the right eye (34% NS, $p = .17$); furthermore, the two areas were fixated more than the left eye (7%, *p*s < .001) and the nose (4%, *p*s < .001), which did not differ from each other ($p = .43$). Hence, the amount of fixations on the eyes increased in general during presentation of the faces, with the total duration of fixations on the two eyes together being almost equal to the mouth for the second to the last but one fixation (41% vs. 46%, respectively). Interestingly, just before or while providing a child's name, PS again fixated to a greater extent on the mouth region, when compared with all other areas (63%, $F_{2.16, 54.2} = 46.11, p < .0001$; mouth vs. others: all ps $< .0001$). The two eye areas were fixated equally longer (14% and 13%, $p = .86$), and did not significantly differ from the nose (5%, ps $> .12$).

The dynamics of fixation patterns is illustrated for four different children faces on Figure 6. Despite a certain amount of variability between different children's face fixations, the mouth always remained the dominant region of interest for PS. Therefore, PFD changed from trial to trial (Figure 6). For example, for face 4, five fixations were sufficient for trial A, but more than 20 were required for trial D. Similarly, for face 2, a single fixation within the mouth region was sometimes sufficient for correct identification (trial E), but fixations on the mouth, right eye, and cheek regions were required for other trials. Despite this inter-trial variability, the dominance of the mouth region is evident for almost every trial.

Comparison of correct and incorrect trials for the prosopagnosic patient PS

For a large number of trials ($N = 353$; chance level at identification is $1/27 = 3.7\%$), the patient either gave a wrong answer (39%) or failed to recognize the child before the end of the trial (5%, Figure 7). The proportion of successful trials varied for the different

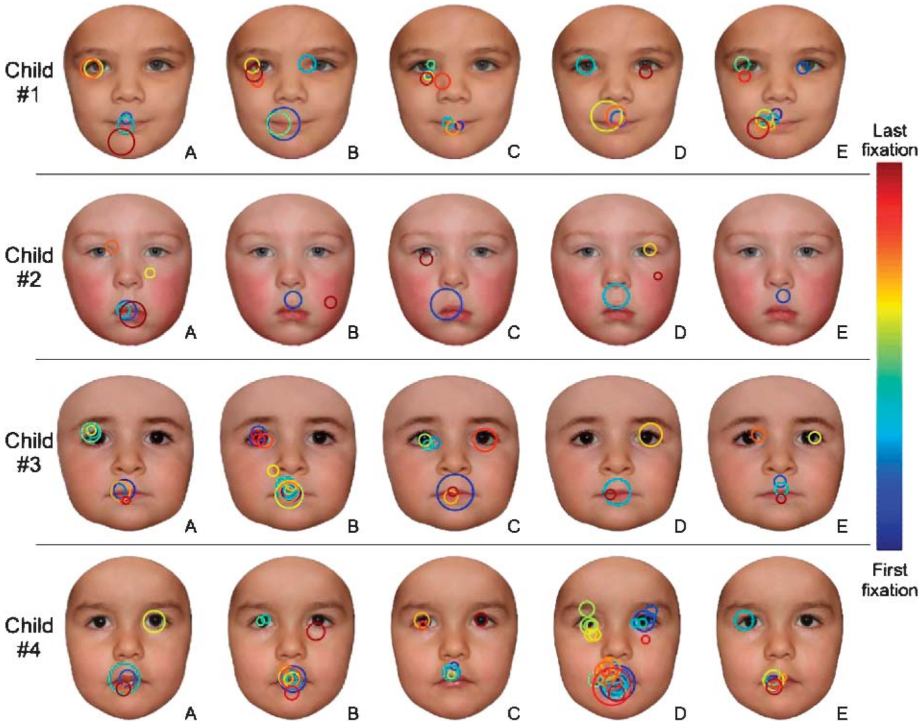

Figure 6. Five representative trials are presented from four different children that the patient recognized in 73, 100, 100, and 92% (top-down) of the trials. Each circle represents one fixation. Its diameter is proportional to the duration of the fixation; its centre is located at the point of fixation. The time sequence of the fixations could be reconstructed from the coloured time scale provided at the right of the figure. The first fixations are represented in dark blue and the last one in dark red.

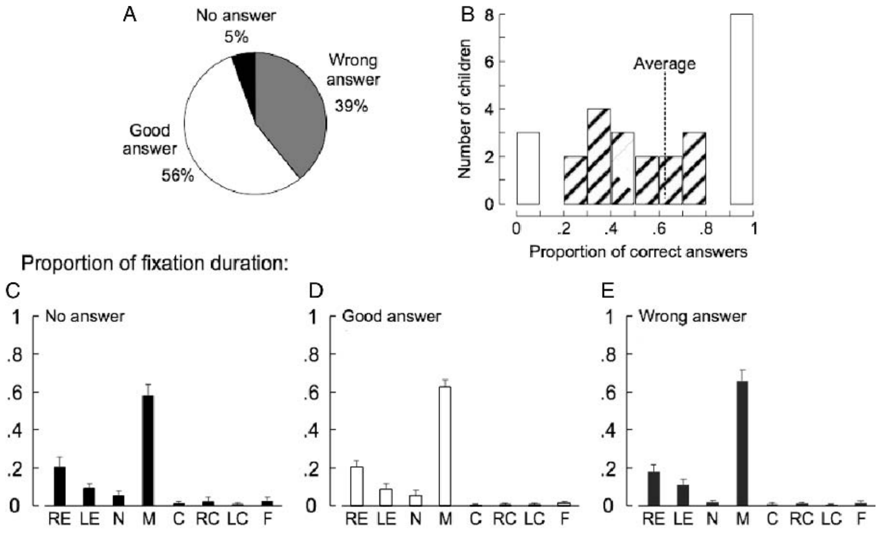

Figure 7. (A) Proportion of correct, incorrect, and no answer trials for the patient PS. (B) Histogram of the proportion of successful trials for the different faces by interval of 0.1. Unhatched bars correspond to participants that the patient either never recognized (<0.1) or always recognized (>0.9). The hatched bars correspond to participants that she occasionally recognized. (C, D, and E) Histogram of the inter-child mean proportion of fixation duration spent fixating on each scoring region for all trials during which she did not answer (C, 17 trials), during which she gave a correct answer (D) or a wrong answer (E). Only the data from the children that she occasionally recognized (hatched bars of B) were used for D and E.

children (Figure 7). PS recognized 8 out of the 27 children more than 90% of the time, but three other children in less than 10% of all instances. The probability that she recognized the 16 remaining children varied from 20 to 80%. These trials on the subset of 16 children were used to compare PFD distribution between the correct and incorrect responses (Figure 7D and E). Interestingly, the scanning behaviour was independent of accuracy: there was no main effect of correctness ($F_{1,15} = 0.28$, $p = .60$), PS did not scan longer for correct as opposed to incorrect trials, and no interaction between correctness and areas of the face fixated arose ($F_{3,45} = 1.88$, $p = .14$), in contrast to a significant effect of area, as expected ($F_{1.93,29} = 344$, $p < .0001$). Indeed, the distribution of PFD among the different scoring regions did not change with the answer PS gave (Figure 7C, D and E). In the three cases (correct, incorrect, or no answer), the mouth region had again the largest PFD among all other regions. Moreover, it is noteworthy that even when the patient scanned the pictures for 60 seconds (trials with no answer), she spent the majority of her time fixating on the mouth region.

Discussion

As hypothesized, the pattern of eye fixations of the prosopagnosic patient PS during a familiar face identification task indicates an overwhelming dominance of fixations on the mouth area of the face. This observation contrasts with the pattern of fixation observed in our normal control participant, who identified all the faces correctly within two fixations located just below the eyes (upper area of the nose). Even though the nature of this study allowed us to test only one valid control participant, it is worth noting that this participant's results are consistent with studies of eye-movement exploration patterns of faces during free exploration encoding and recognition in normal viewers, which clearly shows not only a dominance of the eyes over all other features, including the mouth, but also with a substantial amount of fixation on the nose (e.g. Althoff & Cohen, 1999; Barton *et al.*, 2006; Henderson, Williams, & Falk, 2005; Henderson *et al.*, 2001; see also Guo, Robertson, Mahmoodi, Tadmor, & Young, 2003 for fixations of faces in monkeys). Most importantly, while these studies often present the face stimuli for rather long task explorations in various tasks, a recent experiment showed that during rapid face identification, only two fixations, located on the centre of the face in the upper part of the nose, are sufficient for an optimal performance (Hsiao & Cottrell, submitted). Thus, the results of the normal control tested in this study can be considered as reflecting a normal pattern of fixations during face identification,[1] and contrast the observations for the patient PS.

This abnormal pattern of eye fixations in a single case of acquired prosopagnosia with personally familiar faces has, to our knowledge, never been reported before. A few studies investigated eye-movement patterns during face processing in cases of acquired prosopagnosia, but differed notably from the present study. Rizzo, Hurtig, and Damasio (1987) tested two prosopagnosic patients' scanning patterns of faces and found no qualitative difference with normal controls. However, there was no identification task required (free scanning). Le, Raufaste, & Demonet (2003a) described the eye-movement patterns of the visual agnosic patient SB who was presented with upright, inverted, and scrambled faces, and showed similar fixations as normal viewers in an upright face decision task (see also Le, Raufaste, Roussel, Puel, & Demonet, 2003b). Most recently, Barton, Radcliffe, Cherkasova, & Edelman (2007) recorded eye-movement patterns in a case of acquired prosopagnosia during a famous/non-famous face discrimination task, with upright and inverted faces. Again, this prosopagnosic patient showed the typical advantage of fixation for the eyes and nose over the mouth, as the normal participants of this study, with very few differences in terms of face regions scanned, except for a lack of left visual field bias (Barton *et al.*, 2007). However, these previous studies did not address the same questions as here and used different tasks or no task at all. Most importantly, the patients tested were not as well characterized as PS, and suffered from multiple basic visual impairments besides prosopagnosia, which may explain this lack of significant observations. For instance, the brain-damaged patient studied by Barton *et al.* presents low-level visual defects, including loss of visual acuity, a complete left homonymous hemianopia, object recognition deficits, and achromatopsia.

Even though our observations were made based on a single case and not reported previously, we believe that they may reveal a characteristic signature of acquired prosopagnosia, at least when the perceptual impairment is restricted to faces. Indeed, these observations are in full agreement with the decreased reliance on the eyes relative to the mouth during recognition of learned photographs of faces observed in the same patient PS (Caldara *et al.*, 2005) and for discrimination of unfamiliar faces with matching tasks in another acquired case of prosopagnosia (LR, Bukach *et al.*, 2006, 2008). Interestingly, these patients are prosopagnosic following different lesion localizations

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[1] *Even though it could be argued that the central location of the fixation spot (both in ours and Hsiao & Cottrel's study) increased this dominance of the upper part of the nose over other features, this spot was identical for the patient PS, who nevertheless fixated the mouth first.*

but they have in common the preserved ability to recognize objects (see Rossion *et al.*, 2003; Schiltz *et al.*, 2006 for PS), a pattern that is extremely rare in the literature (e.g. De Renzi, 1986; one case in Sergent & Signoret, 1992). The pattern observed in these studies may thus be limited to, or highly salient, in the so-called 'pure' cases of prosopagnosia, reflecting the nature of their selective deficit at recognizing faces.

Here, while the mouth is by far the area of the face most attended to, the data show that the patient PS also relies substantially on the eyes for face identification, an area that was not identified as being diagnostic at all during the response classification experiment of Caldara *et al.* (2005) with PS. There are two possible accounts for this difference between experiments. The present data could suggest that the eyes were also fixated substantially during the response classification experiment with 'Bubbles', but since they did not convey diagnostic information for the patient, this area was not revealed in the response classification image. This may explain why, in the present experiment, the patient reliably fixated the mouth prior to individual identification (Figure 5). However, against this explanation, we found no difference in the distribution of fixations for correct and incorrect trials here, suggesting that, when the eyes were used to identify the children's faces in the present study, they were not less diagnostic than the mouth. Hence, an alternative explanation of this difference between studies is that the patient uses the eyes *relatively* more when she has to identify personally familiar faces than the learned photographs in the 'Bubbles' study of Caldara *et al.* (2005). This could be due to a difference in the quality of representation of the faces, or to stimulus factors. For instance, we note that faces were presented in colour in the present experiment, as opposed to greyscale in our previous study (Caldara *et al.*, 2005). Since the patient's colour perception is well preserved (Sorger *et al.*, 2007) and can be used to discriminate faces (Ramon & Rossion, 2007), local information of the faces (e.g. eye colour) could have been used as an additional cue in the present study, reinforcing the fixations on the eye regions. A response classification experiment with personally familiar face photographs of the patient PS could help clarifying this issue in the future. All in all, it remains that when the patient has to identify familiar faces, the area around the eyes appears to be much less diagnostic and fixated less than the mouth, which is in concert with the outcome of the 'Bubbles' study.

A more striking difference between the outcome of the response classification study and the observed fixation patterns was obtained for the control participant: she did not fixate exactly *on* the eyes, as identified with response classification (Caldara *et al.*, 2005; Gosselin & Schyns, 2001; Haig, 1985, 1986, see also Sekuler *et al.*, 2004) but rather on the centre of the face, slightly below the eyes (upper nose area for normal faces). This observation is consistent with other evidence of eye fixation location during rapid face identification (Hsiao & Cottrell, submitted). It would be difficult to argue that this fixation point on the face for normal viewers is the local most diagnostic spot, in itself, to identify faces (i.e. where individual faces would differ most). As a matter of fact, it is not identified in response classification experiments for normal viewers or ideal observers. However, in line with other sources of evidence (Hsiao & Cottrell, submitted; Jeffreys, Tukmachi, & Rockley, 1992), we suggest that this eye fixation location – central location on the upper nose, in between the eyes – is the optimal spot to simultaneously process the other multiple potential diagnostic features that are located close to this fixation point on the face. In other words, even when fixating this central upper nose area, the normal viewer most probably relies on information located on the two eyes (predominantly) and the mouth. This illustrates how response classification and gaze behaviour recordings may complement each other: while the former will identify the local spots that are most diagnostic for face identification, the latter indicates that when all information is available simultaneously, the viewer rather concentrates on the optimal viewing point for processing all of these features, in particular in the upper area, within the same fixation.

Commonalities and differences with other face processing disorders

As indicated in the Introduction, reduced fixation on the eyes is also characteristic of patients with social disorders such as autistic children (Klin *et al.*, 2002; Pelphrey *et al.*, 2002). However, in the case of autism, there is an active avoidance of eye-contact, and the presence of diagnostic information in the eyes even appears to increase the tendency of autistic patients to saccade away from this region (Spezio *et al.*, 2007a). In contrast, the present data demonstrate that the prosopagnosic patient PS (a person with extremely high social skills, as further emphasized by her profession) spontaneously looks at the eyes whilst attempting to identify the faces of the children. Her pattern of face scanning is thus clearly different from what is typically observed in autism.

The present observations also help to differentiate the behaviour of our acquired prosopagnosic patient from a recent case report of a patient with bilateral amygdala damage (Adolphs, Tranel, Damasio, & Damasio, 1994) who does not use information from the eye region when judging facial expressions (Adolphs *et al.*, 2005). This patient's deficit was directly related to a lack of spontaneous fixations on the eyes during free viewing of faces, as also observed during normal conversations with such patients (Spezio *et al.*, 2007b). When told explicitly to use the eyes to categorize facial expressions, the amygdala patient's judgments became entirely normal. Accordingly, the authors concluded that the patient's impairment was not due to a visuoperceptual deficit of processing information from the eyes, but instead to a failure by the amygdala to 'direct her visual system to seek out, fixate, pay attention to and make use of such information to identify emotions' (Adolphs *et al.*, 2005). In contrast, we found that the acquired prosopagnosic PS spontaneously and substantially fixated the eyes of faces, as she does under real life circumstances.[2] This indicates that her deficit has a different functional locus than the reported patient with bilateral amygdala damage, an argument which is reinforced by the absence of amygdala lesion or other areas related to eye-gaze processing (i.e. Superior Temporal Sulcus, STS) in PS's brain (Sorger *et al.*, 2007). Moreover, her ability to categorize facial expressions is almost in the normal range, in contrast to her massive face identification impairments (Rossion *et al.*, 2003). In summary, the present data strongly suggest that the reduced reliance on the eyes observed in acquired prosopagnosia (Bukach *et al.*, 2006, 2008; Caldara *et al.*, 2005) is associated with different underlying causes and neurofunctional mechanisms than in autism or bilateral amygdala damage.

The nature of the eyes' reduced diagnosticity in acquired prosopagnosia

Why acquired prosopagnosic patients do not fixate and use information from the upper area of the face, in particular the eyes, during familiar face identification or unfamiliar face discrimination? Why do they utilize the mouth area instead? We have already

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[2] *Even though this is anecdotal, there is no evidence that PS is avoiding gaze contact during conversations. Yet, she often mentions and describes characteristics of the mouth when referring to people's physical appearance.*

discussed this issue in our previous work (Caldara *et al.*, 2005), but the present data promote a better understanding.

First of all, we can rule out the hypothesis that prosopagnosic patients would simply not look at the faces' eyes to avoid the social embarrassment of not recognizing others and being accused of 'staring'. Both prosopagnosic patients PS and LR (Bukach *et al.*, 2006; Caldara *et al.*, 2005) are two extremely social individuals who do not avoid gaze contact at all. Moreover, the patient PS recognizes the children in the kindergarten, and there would be no reason to avoid gaze contact with them. On a more scientific basis, the data collected here rule out this explanation simply because the patient also spontaneously fixated the eyes, albeit to a much lesser extent than the mouth.

A second account of this abnormal eyes/mouth balance in fixating and using facial cues calls upon low-level perceptual factors. That is, prosopagnosic patients may fail to use information located in the upper part of the face because of the presence of upper visual field defects, caused by their ventral lesions which may extend to primary visual areas (see e.g. Bouvier & Engel, 2006; Meadows, 1974). As a matter of fact, PS has a small left paracentral scotoma in the upper visual field (see Sorger *et al.*, 2007 for details), like a large number of acquired cases of prosopagnosia (Bouvier & Engel, 2006). However, this factor cannot account for her behaviour during face identification since she is given a fair amount of time to answer, during which she can move the eyes freely. Moreover, this lack of reliance on the eyes has also been observed with LR, a case of prosopagnosia following an anterior right temporal lesion, who has a full visual field (Bukach *et al.*, 2006). Finally, if anything, the present data show that PS does actually fixate the upper part of the faces.

A third account, also low-level, would be that relative to the mouth, the eyes convey diagnostic information at a higher degree of resolution; that is, requiring resolving higher spatial frequencies than the mouth. However, spatial frequencies were manipulated in the 'Bubbles' study, and there was no evidence of a specific impairment of the patient PS for information contained within higher or lower bands of spatial frequencies (Caldara *et al.*, 2005). More generally, the literature does not provide unequivocal evidence for either low or high spatial frequency processing defects in acquired prosopagnosic patients, some studies showing reduced contrast sensitivity in the high frequency range for non-facial stimuli in prosopagnosic patients (Barton, Cherkasova, Press, Intriligator, & O'Connor, 2004; Rizzo, Corbett, Thompson, & Damasio, 1986), but others reporting cases of prosopagnosic patients having a marked deficit at resolving mostly low spatial frequencies on face stimuli (e.g. Sergent & Villemure, 1989).

Thus, overall, one can safely assume that the patient's reduced reliance on the eyes during face identification is not due to low-level visual problems, social factors, or a *failure* to orient towards and fixate the areas of the eyes. Moreover, it cannot be attributed to other areas such as the mouth conveying enough diagnostic information, because PS's face identification performance remains well below normal controls, and she is very slow. Finally, when increasing difficulty of the identification for the normal control participant by using anti-caricatures of the faces, there was no increase of fixations of the mouth at all – if anything, the normal viewer focused even slightly above, with most fixations in between, the eyes of the face. To put it simply, during face identification, the eyes of the face do not appear to be of a great help compared to the mouth for PS, unlike for our control participant and normal viewers in general.

Our favourite theoretical account of this phenomenon, explicitly stated first in Caldara *et al.* (2005) and refined recently (Ramon & Rossion, 2007), calls upon high-level visual processes of faces. We suggest that the highest diagnosticity of the eye area of the face for normal viewers, an area which contains multiple (pairs of) features over a reduced space (i.e. eyebrows, eyelid, eyelash, eyeball, pupil, and iris), critically depends on the ability of the face processing system *to simultaneously represent multiple elements of a face as an individual perceptual unit*. This would be our adapted definition of holistic face perception, largely inspired and derived from early and more recent theoretical proposals (Galton, 1883; Sergent, 1984; Tanaka & Farah, 1993). Holistic face perception is usually measured through the interactivity of facial features (Sergent, 1984; Tanaka & Farah, 1993); for instance, using the so-called face composite paradigm (Young, Hellawell, & Hay, 1987). In one version of this paradigm, the viewer fixates the top part of a face stimulus and perceives it as slightly different if it is aligned with different bottom parts (e.g. Goffaux & Rossion, 2006; Le Grand, Mondloch, Maurer, & Brent, 2004; Michel, Rossion, Han, Chung, & Caldara, 2006). Hence, by fixating one part of the face, the viewer's perception is influenced by the other parts, a hallmark of holistic face perception.

According to this hypothesis, in identification tasks, the diagnosticity of the upper area of the face would depend more heavily on holistic face perception than the lower area, mostly because it includes more elements over a small space. Hence, the primary cause of the face impairment for PS, and most probably for other acquired prosopagnosic patients, would be the loss of holistic face perception, preventing to perceive multiple elements of an individual face as a unit. As a result, the patient PS would have to process faces differently: local feature by local feature. This analytical mode of processing mainly affects the dominant diagnosticity of the region encompassing the eyes, which in-turn promotes increased reliance on the mouth when compared with normal observers.

Importantly, this hypothesis does not imply that the eyes of the face have completely lost their diagnosticity. For instance, if diagnostic information can be extracted locally (e.g. eye colour) and predictably, and/or if the ambiguity inherent to the presence of multiple features in the absence of holistic face perception is resolved by telling the patient where to attend to, the patient may well rely on the eye area. For instance, both the patients PS and LR appear to be able to use information on the eyes if they are told to attend to particular information in this area during a discrimination task between two faces (Bukach *et al.*, 2006; Ramon & Rossion, 2007). However, face identification requires to compare a percept to stored representations, and to find the best match. As prosopagnosic patients' *individual* representations of faces are composed of local elements, it is conceivable that each feature of the eye region, in isolation, is less diagnostic than the mouth – a relatively well-isolated feature of the face, associated with characteristic motion and the person's voice. Hence, the patients will privilege the mouth simply because they have a stronger representation of the mouth for most faces (except if a *local* cue on the eye or another location is highly diagnostic of a particular identity, such as a specific colour for instance). The repeated sampling of the region of the face with the strongest representation in internal memories for PS – here the mouth – is thus the most effective strategy for resolving ambiguity in the process of identifying the children's faces.

Admittedly, this theoretical proposal is still quite speculative at this state of knowledge. However, it is consistent with previous behavioural studies of prosopagnosia, and the contrast between PS's and the normal control's fixation patterns observed here.

First, our hypothesis of a causal link between holistic face perception and our observations (eyes/mouth unbalanced use and fixation) is consistent with a wide body of evidence showing a loss of the ability to process faces holistically in acquired prosopagnosia (e.g. Barton, Press, Keenan, & O'Connor, 2002; Boutsen & Humphreys, 2002; Joubert *et al.*, 2003; Levine & Calvanio, 1989; Saumier, Arguin, & Lassonde, 2001; Sergent & Signoret, 1992). As stated, these patients usually suffer from other deficits than face perception, for instance showing visual integrative agnosia (e.g. Riddoch & Humphreys, 1987) in addition to their face perception deficit. It is important to understand that in the present case, as in LR (Bukach *et al.*, 2006), we are here referring to a patient who does not present object recognition deficits, and can integrate features to succeed in basic-level categorization. For instance, the patient PS can detect faces normally (e.g. Schiltz *et al.*, 2006), even when this requires feature integration, such as in two-tone 'Mooney' pictures (Busigny & Rossion, in preparation). PS's prosopagnosia is better characterized as a defect at representing simultaneously multiple elements of a face as an *individual* perceptual unit, and we have independent evidence that she does not show typical holistic processing of faces behaviour on familiar and unfamiliar faces (Ramon & Rossion, 2007).

Second, as we noted above, the control participant's data indicate that, even though the eyes are most diagnostic for face identification in general, the optimal fixation point is not *on* the eyes, or focused *on any* feature. Rather, it is located in between and slightly below the eyes, in the centre of the upper area of the face. This normal viewer makes very few eye-movements in fact, fixations being localized on a small area on the top of the nose. This is even the case for the identification of the anti-caricatures, even though the optimal fixation point for identification is slightly elevated. This absence of eye-movements between features with the presence of a central optimal fixation point suggests a form of holistic face processing, as opposed to an analytical behaviour: the different facial features can be perceived as a whole template from that fixation point, so that there is no need to move the eyes much. This suggestion is consistent with recent evidence that holistic face perception, measured during the face composite paradigm, is independent of eye-movements (de Heering, Rossion, Turati, & Simion, 2008, this issue). It also agrees fully with the findings of Schwarzer and colleagues that children and adults who apply a holistic approach to face identification (i.e. taking into account multiple features for face categorization, see Schwarzer, Huber, & Dummler, 2005) focus mainly on the nose and eye area of the faces. In contrast, and much like the patient PS in the present study, analytical processors appear to have longer fixation durations and focus on a single diagnostic feature at a time (eyes, nose, and then the mouth). Here, the patient PS did not only fixate the centre of the mouth extensively, but she moved the eyes from the mouth to the eyes back and forth, making more eye-movements than the control. Moreover, contrary to the normal control and quite interestingly, PS's fixations fall right on the centre of each feature, not in between features (Figure 2). This is highly suggestive of a form of processing that is deprived of holistic face perception, i.e. analytical (see also Schwarzer *et al.*, 2007 for congruent evidence in cases of congenital prosopagnosia).

Finally, and also concordant with our view, behavioural studies with normal viewers indicate that the area of the eyes is processed more holistically than other face features (e.g. Donnelly & Davidoff, 1999; Leder, Candrian, Huber, & Bruce, 2001; Rakover & Teucher, 1997). Here, we suggest that this area is not only processed more holistically, but also its diagnosticity for face identification is highly *dependent* on holistic perception. That is, the development of an efficient way of coding and discriminating individuals based on this region of the face *necessitates* a mechanism that allows perceiving these features as a single template, rather than having to deal with each feature individually.

Ongoing and future work with cases of prosopagnosia such as PS, as well as normal participants, will attempt to clarify further this view, which is largely inspired from single-case studies of brain-damaged prosopagnosic patients but helps us to understand the nature of the normal face perception system.

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