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Research report

Acquired prosopagnosia abolishes the face inversion effect

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ABSTRACT

Individual faces are notoriously difficult to recognize when they are presented upside-down. Since acquired prosopagnosia (AP) has been associated with an impairment of expert face processes, a reduced or abolished face inversion effect (FIE) is expected in AP. However, previous studies have incongruently reported apparent normal effects of inversion, a decreased or abolished FIE, but also a surprisingly better performance for inverted faces for some patients. While these discrepant observations may be due to the variability of high-level processes impaired, a careful look at the literature rather suggests that the pattern of FIE in prosopagnosia has been obscured by a selection of patients with associated low-level defects and general visual recognition impairments, as well as trade-offs between accuracy and correct RT measures. Here we conducted an extensive investigation of upright and inverted face processing in a well-characterized case of face-selective AP, PS (Rossion et al., 2003). In 4 individual face discrimination experiments, PS did not present any inversion effect at all, taking into account all dependent measures of performance. However, she showed a small inversion cost for individualizing members of a category of non-face objects (cars), just like normal observers. A fifth experiment with personally familiar faces to recognize confirmed the lack of inversion effect for PS. Following the present report and a survey of the literature, we conclude that the FIE is generally absent, or at least clearly reduced following AP. We also suggest that the paradoxical superior performance for inverted faces observed in rare cases may be due to additional upper visual field defects rather than to high-level competing visual processes. These observations are entirely compatible with the view that AP is associated with a disruption of a process that is also abolished following inversion: the holistic representation of individual exemplars of the face class.

1. Introduction

Individual faces are notoriously difficult to discriminate and recognize when they are presented upside-down (e.g., >Hochberg and Galper, 1967; Yin, 1969). This phenomenon has been known for decades and has generated tens or perhaps hundreds of studies in cognitive (neuro)science comparing behavioral performance and/or neural responses to upright and inverted face stimuli. While researchers still debate the cause(s) of this face inversion effect (FIE), most if not all authors in the field would acknowledge that inversion disrupts fundamental processes underlying our expertise at

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processing faces. Understanding the nature of the FIE is thus a major challenge for researchers in this field (Rossion, 2008).

Another potential way to understand the nature of face processes through their disruption is by studying the behavior of brain-damaged patients who can no longer recognize individual faces, i.e., acquired prosopagnosia (AP). Prosopagnosia is classically defined as the inability to recognize individual faces following brain damage, an impairment which cannot be attributed to intellectual deficiencies or low-level visual problems (Quaglino and Borelli, 1867; Bodamer, 1947; Rondot and Tzavaras, 1969). The nature of the face processing impairment in prosopagnosia has also been debated in the literature for decades (e.g., Rondot and Tzavaras, 1969; Damasio et al., 1982; Sergent and Signoret, 1992). While some authors have emphasized the variety of functional deficits among patients (Sergent and Signoret, 1992; Schweich and Bruyer, 1993), there are striking similarities among many cases of prosopagnosia, even when the localization of their brain lesions differs greatly. In many reports, AP has been associated with a deficit in holistic/configural face processing, i.e., a defect at integrating simultaneously the multiple features of a face into a single global perceptual representation (e.g., Galli, 1964; Levine and Calvanio, 1989; Sergent and Villemure, 1989; Sergent and Signoret, 1992; Saumier et al., 2001; Boutsen and Humphreys, 2002). More recently, it has also been found that prosopagnosic patients have particular difficulties at extracting diagnostic information from the eyes (Caldara et al., 2005; Bukach et al., 2006), a region of the face that is made of multiple elements, or at perceiving relative distances between features (Barton et al., 2002). These two aspects of prosopagnosia may also be related to a loss of holistic face processing (Rossion, 2008).

How do AP patients process upright and inverted faces? In principle, clarifying this relationship between prosopagnosia and inversion is potentially important because it could shed light on both the nature of face inversion and prosopagnosia, in particular reinforcing or questioning the view that the (in)ability to process individual faces holistically is at the heart of the AP syndrome.

If the outcome of brain damage on putative expert face processes is as detrimental as inverting the face stimulus for normal observers, so to speak, one would expect that AP patients do not show a normal FIE: it should be seriously reduced or even abolished. However, even when considering only the experiments performed with whole upright and inverted faces in individual discrimination/recognition tasks, four different outcomes have been observed: (1) an *absence of inversion cost* in several cases (McNeil and Warrington, 1991, case 2 in accuracy and RTs; Boutsen and Humphreys, 2002, patient HJA in accuracy; Delvenne et al., 2004, patient NS in accuracy and RTs); (2) a *reduced FIE* in two cases tested with manipulations of local and relational cues for individualizing faces (Barton et al., 2003, patient TS in accuracy; Bukach et al., 2006, patient LR in accuracy); (3) a *normal effect* in one patient (Anaki et al., 2007, patient DBO in accuracy and RTs); and (4) a *reverted inversion effect*, namely a better performance for inverted faces in some cases (Farah et al., 1995a, 1995b; de Gelder and Rouw, 2000a, 2000b, patient LH in accuracy and RTs; de Gelder et al., 1998, patient AD in accuracy). In addition, there are ambiguous cases (e.g., Riddoch et al., 2008, patient FB, reverted trend in RTs for same responses, but normal effect with different responses) and inconsistencies in the results reported for the same patients in the literature. For example, the (prosop)agnosic patients CR, SM and RN were tested in several studies (Gauthier et al., 1999; Marotta et al., 2002; Behrmann et al., 2005). Gauthier et al. (1999) reported large inversion effects in both accuracy and RTs for CR and SM. In another study (Marotta et al., 2002), CR still performed better with upright faces, but was significantly faster for inverted faces, contrary to controls, suggesting a speed-accuracy trade-off. In that study, the patient RN did not show any effect in accuracy but a normal inversion effect in RTs (Marotta et al., 2002). However, most recently, all three patients, considered as a group, were reported as performing slightly better and faster with inverted faces (Behrmann et al., 2005).

Thus, overall, the outcome of inversion on individual face processing in AP remains unclear. One way to account for the variability across patients is by acknowledging the great variability in terms of functional impairments of AP, following different lesion localization(s) and aetiologies, as well as putative compensatory strategies (Sergent and Signoret, 1992; Schweich and Bruyer, 1993). However, when considering the literature on face inversion and prosopagnosia attentively, one cannot help noting a number of methodological issues in patient selection, tasks performed, variables measured and analyzed, as well as possible overinterpretations of some observations. As a result, the variety of outcomes reported about inversion effects in prosopagnosia may equally well have been created by the different kinds of experiments performed rather than reflecting a true functional variability in terms of *face* processes. This argument is supported by several observations. First, as noted above, there are inconsistencies in the results reported for the same patients in the literature (e.g., Gauthier et al., 1999; Marotta et al., 2002; Behrmann et al., 2005). These opposite patterns across studies, observed during individual face matching tasks in the same brain-damaged patients, cast doubts on the conclusions that can be drawn from these studies at least regarding the FIE in prosopagnosia. It is worth noting also that these cases were close to chance level with upright faces in several experiments, making difficult to draw clear conclusions. Second, many studies do not measure or report correct RTs during individual face processing tasks (e.g., de Gelder et al., 1998; de Gelder and Rouw, 2000a, 2000b; Boutsen and Humphreys, 2002). Yet, it is known that when having to match/discriminate individual faces, prosopagnosic patients can achieve reasonably high scores by using unnatural (i.e., analytical) strategies (Davidoff and Landis, 1990; Farah, 1990), which may be revealed by abnormally long RTs. Moreover, correct RTs are a highly sensitive measure of the effects of face inversion in normal observers (see Rossion, 2008). Most importantly, when RTs are measured in studies of face inversion in prosopagnosia, they are rarely considered with respect to accuracy to rule out potential speed-accuracy trade-offs effects (e.g., Marotta et al., 2002), or combined with accuracy to obtain a global face inversion index. Third, most studies do not compare the processing of upright and inverted faces to non-face objects presented at the two orientations (McNeil and Warrington, 1991; Farah et al., 1995a, 1995b; Marotta et al., 2002; Delvenne et al., 2004;

Behrmann et al., 2005; Anaki et al., 2007). However, it may be important to monitor for general effects of picture inversion, which may not be directly related to the ability to process faces. For instance, LH, the only patient who clearly presents a better performance for inverted than upright faces both in accuracy and RTs (Farah et al., 1995a, 1995b), shows the exact same pattern for pictures of non-face objects (shoes; de Gelder and Rouw, 2000a). Strangely enough, these non-face objects do not even lead to inversion costs for normal observers (de Gelder et al., 1998). This suggests that LH's relative inversion superiority in processing inverted items may be due to a general visual impairment rather than face processes *per se* (e.g., his massive upper visual field defects, see Levine and Calvanio, 1989). Fourth, tasks and stimuli used differ greatly across studies: same/different (AX) discrimination or 2-alternative forced choice paradigms (ABX), with simultaneous presentations of all items or delayed presentations (AX; ABX), etc. During same/different (AX) discrimination tasks, response biases can arise (e.g., the patient responding systematically that the faces are identical), making impossible to interpret the results on ''different'' trials (e.g., Gauthier et al., 1999; Boutsen and Humphreys, 2002). Moreover, large variations in presentations times have been used during delayed matching tasks [from 400 msec (Anaki et al., 2007) to 10 sec (Farah et al., 1995a, 1995b)]. Fifth, another major factor limiting the interpretation of the outcome of previous experiments is that all the patients tested with upright and inverted faces so far present clear general visual recognition problems, in particular with objects (excepted FB, Riddoch et al., 2008) besides their face recognition impairments, preventing to assess clearly the relative inversion costs for faces and non-face objects. Finally, as noted above, these patients present important low-level visual defects (McNeil and Warrington, 1991; Farah et al., 1995a, 1995b; Boutsen and Humphreys, 2002; Delvenne et al., 2004; Anaki et al., 2007), as often found in cases of prosopagnosia following brain damage.

Given all these reasons, we aimed at reinvestigating the question of how AP patients process upright and inverted faces, in order to shed light on both the nature of the FIE and AP. We took advantage of the opportunity to test extensively a well-described case of AP with no object recognition impairment, and largely preserved low-level visual abilities (PS, Rossion et al., 2003). The patient was tested in 5 different behavioral experiments with upright and inverted faces and her results were contrasted with a carefully selected population of age-matched controls for each experiment. We used different stimuli and paradigms, avoided response biases (2-alternative forced choice matching tasks), measured both accuracy rates and correct response times to assess speed-accuracy trade-offs and display global indexes of inversion costs, and compared the effect of inversion to another category of mono-oriented stimuli (Experiments 3 and 4). Finally, given that the patient is in daily contact with a large set of homogenous faces (children of a kindergarten), we also had the opportunity to assess for the first time the FIE in prosopagnosia during familiar face recognition. Over all experiments, the results were highly consistent, showing an absence of face inversion cost for the prosopagnosic patient PS. There was no hint of inversion superiority. We discuss these observations in the context of previous case studies and the nature of the FIE, arguing that a significant reduction of the FIE in prosopagnosia is not only the most observable pattern following a careful look at the literature, but it is also the most plausible, from a theoretical point of view.

2. Participants

2.1. PS

The prosopagnosic patient PS' behavioral and neural profiles have been described in details in several previous studies (e.g., Rossion et al., 2003; Caldara et al., 2005; Sorger et al., 2007). Briefly, PS was born in 1950 and sustained a closed head injury in 1992 that left her with extensive lesions of the left mid-ventral (mainly fusiform gyrus) and the right inferior lateral occipital cortex [see (Sorger et al., 2007) for all information about the patient's lesions]. PS' only continuing complaint is a profound difficulty in recognizing familiar faces, including those of her family when they are presented out of context [see Table 1 in (Rossion et al., 2003) for the neuropsychological profile of the patient]. This impairment in face recognition and individual face discrimination has been formally established in several behavioral studies with classical neuropsychological tests (Benton Face Recognition Test, Benton et al., 1983; Warrington Recognition Memory Test, Warrington, 1984) as well as individual face matching and recognition computer tasks (see Rossion et al., 2003; Caldara et al., 2005; Schiltz et al., 2006; Orban de Xivry et al., 2008). Importantly, PS does not present any difficulty in recognizing and discriminating non-face objects, even at the subordinate level and when response times are considered (Rossion et al., 2003; Schiltz et al., 2006). Her visual field is almost full (small left paracentral scotoma, see Sorger et al., 2007), her visual acuity is below normal but good (.8 for both eyes as tested in August 2003) and her color perception is in the normal lower range (see Sorger et al., 2007).

2.2. *Control participants*

Healthy control participants tested in this study were age-matched with PS. None of them had a history of neurological or vascular disease, head injury or alcohol abuse, nor did they display cognitive complaints. All of them signed a consent form explaining the general goal of the experiment. The number of control participants and their age differ slightly across the experiments and are consequently referenced in the methods of each experiment.

3. Experiments

PS and the control participants were administered with a set of 5 experiments. Apart for the first experiment, the stimuli were presented using E-prime 1.1 (Schneider et al., 2002) on a 15in laptop display, with participants being located approximately 40 cm from the screen. Participants were generally asked to provide a binary response using the keyboard of the laptop computer. Percentages of correct responses and average response times on correct trials were analyzed. RTs that were longer than 2 SDs of the mean were discarded. For intra-subject and intra-group statistical analysis, we used respectively classical independent sample *t*-tests and paired sample *t*-tests. These analyses were conducted by Statistical Package for the Social Sciences 14.0 (SPSS 14.0) within the framework of one-tailed hypothesis (.05 *p* value). To compare the results of PS to the control participants, we used the modified *t*-test of Crawford and Howell (1998) for single-case studies. This procedure decreases the type 1 error as it tests whether a patient's score is significantly below controls by providing a point estimate of the abnormality of the score. Here we used a .05 *p* value within the framework of a unilateral hypothesis. Consequently, all scores associated with a *p* value under .05 were considered as reflecting an abnormal result. Analyses were conducted with a computerized version of the Crawford and Howell's method: *SINGLIMS.EXE: Point estimate and confidence limits on the abnormality of a test score* (Crawford and Garthwaite, 2002).

3.1. Experiment 1: BFRT upright and upside-down

Experiment 1 consists in the administration of the classical Benton Face Recognition Test (BFRT) (Benton et al., 1983), presented infra. The reasons why this test was administered are the following. First, it is a classical test of individual face discrimination, reported in many cases of AP. Second, it is highly sensitive at revealing face impairments in such patients. Benton and colleagues classify the results of this task in four types of profiles: normal (score between 41 and 54), borderline (39–40), moderately impaired (37–38) and severely impaired (<37), chance level being 25/54. Most cases of AP have severely impaired scores in the BFRT (e.g., SM: 36/54, CR: 36/54, Gauthier et al., 1999; TS: 22/54, Barton et al., 2003; 008: 25/54, 004: 32/54, 005: 35/54, 006: 32/54, Barton et al., 2004). However, as noted by Benton himself (1980), some patients can reach close to normal or normal performance at the BFRT (e.g., Case 2: 40/54, McNeil and Warrington, 1991; CR: 40/54, Marotta et al., 2002; 007: 39/54, 009: 43/54, Barton et al., 2004; NS: 40/54, Delvenne et al., 2004; LR: 49/54, Bukach et al., 2006; DBO: 42/54, Anaki et al., 2007). Yet, when response times are taken into account, these patients often appear to rely on a slow analysis of the faces (Case 2: mean RT by trial 82 sec, McNeil and Warrington, 1991; NS: mean RT by trial 55 sec, Delvenne et al., 2004; LR: mean RT by trial 55 sec, Bukach et al., 2006; for information, normal controls perform this test in 5–7 min, or 13–19 sec by trial on average, see e.g., Joubert et al., 2008). Thus, even though this test has been criticized by some authors (Duchaine and Weidenfield, 2003), the BFRT appears to be a highly sensitive test to diagnose prosopagnosia, providing that both accuracy rates and global RTs are considered, and acknowledging that the BFRT is not a test of face memory (see Benton, 1980).

PS performed the BFRT for the first time shortly after her accident as part of her neuropsychological assessment, and obtained a dramatic score of 27/54 (Rossion et al., 2003). Here, PS was administered with the BFRT once again, in the two orientations, for the goal of the present study. The first test was one in the upright orientation (23/11/2006), and the second test in the inverted orientation (12/06/2007). In both cases, she took more than 30 min to perform the test, while normal participants performed the test in 6–8 min on average.

3.1.1. *Materials and methods*

3.1.1.1. Control participants. Eleven healthy control participants (8 females) were selected (mean age: 57.55; SD: 7.7).

3.1.1.2. Stimuli. The stimuli used in the experiment consisted in the original version of the BFRT (Fig. 1). We presented the test in the original upright orientation and a second time (one day later for the controls) in the inverted position. The order for orientation was not counterbalanced because we wanted control participants to perform the BFRT in the same order as PS. If anything, presenting the test at inverted orientation the second time the next day could only have improved their performance for the inverted relative to upright orientation, which runs counter to our hypothesis of finding a strong inversion effect in these participants than for the patient PS.

3.1.1.3. Procedure. The BFRT is divided into two parts. In the first part (6 trials), the participant has to match an unknown face with the same face amongst five distracters. The probe is exactly the same photograph than the target (same viewpoint, same lighting). The answer is an oral answer and consists in a number from 1 to 6 corresponding to the position of the probe. In the second part (16 trials for the long version), the participant has to match an unknown face with three other pictures of this face amongst three distracters. In this section, either the viewpoint or the direction of the lighting changes, making the task more difficult. The participant has to provide orally three numbers that correspond to the position of the selected probes.

3.1.2. *Results*

Analyses of average accuracy rates (paired sample *t*-test) revealed a massive FIE for the control participants: 84.7% for upright faces and 69.4% for the inverted orientation ($t_{10} = 8.94$, $p < .001$). In contrast, PS obtained a lower score in the upright condition in comparison to the control participants (72.2%, $t = 1.99$, $p < .05$), but she performed in the normal range for the inverted condition (70.4%, $t = .12$, $p = .45$). Importantly, PS did not present any difference between the upright and the inverted orientation ($t_{21} = .271$, $p = .39$) (Fig. 2).

3.1.3. *Discussion*

PS' score at the test in the normal orientation (39/54; 72.2%) reveals a mild impairment compared to the BFRT norms, but she was extremely slow and impaired relative to the participants' average performance in our sample (84.7%, corresponding roughly to 46/54 on average). While, as expected, participants showed a massive decrease of performance with inverted faces, PS' score with inverted faces was virtually identical as for upright faces, to the point that it did not longer differ (in terms of accuracy rates) from the normal population for inverted faces. We also note that her score was clearly above chance level in the BFRT test, so that her absence of inversion effect could not be attributed to a floor effect. To our knowledge, the BFRT was not presented before in the inverted

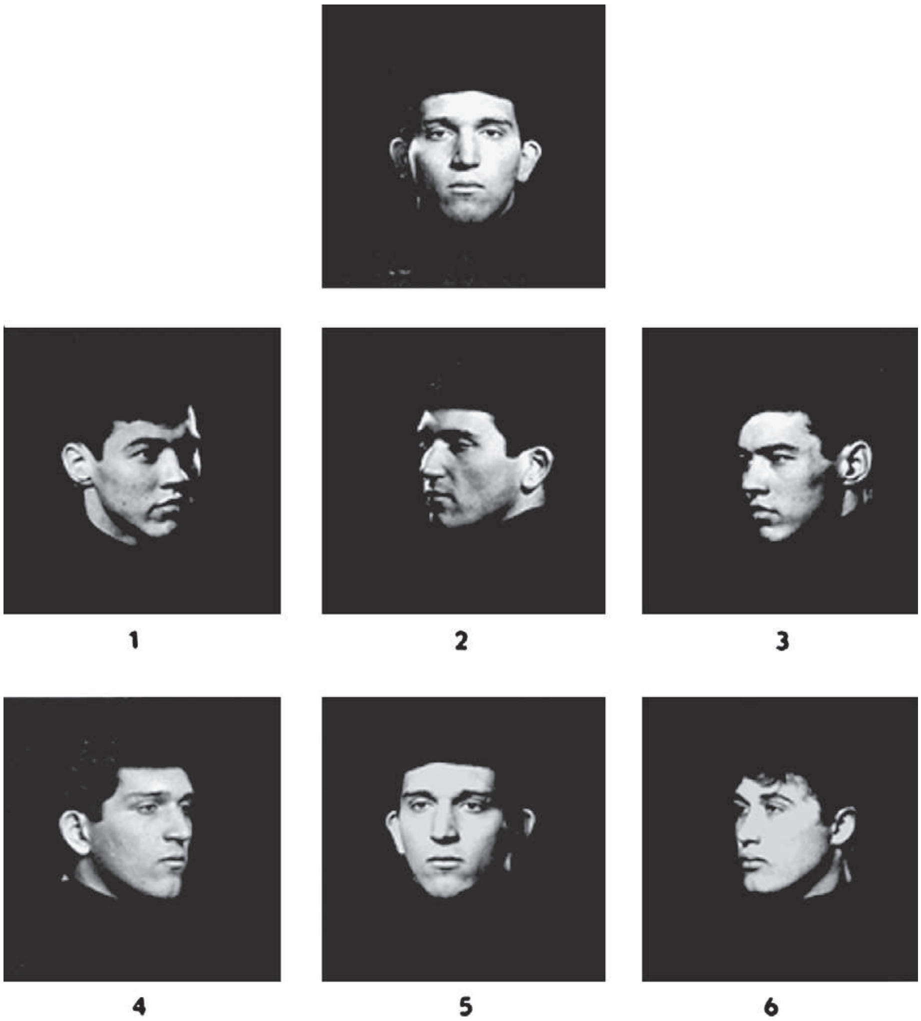

Fig. 1 – Examples of stimuli used in the BFRT (Benton et al., 1983).

orientation to prosopagnosic patients, except by McNeil and Warrington (1991). Case 2 of their study obtained the same results in the upright and in the inverted orientation (respectively 40/54 and 41/54), compatible with the present observations. The next experiment was aimed at testing this lack of FIE with face photographs presented in a computer screen, measuring RTs for each trial.

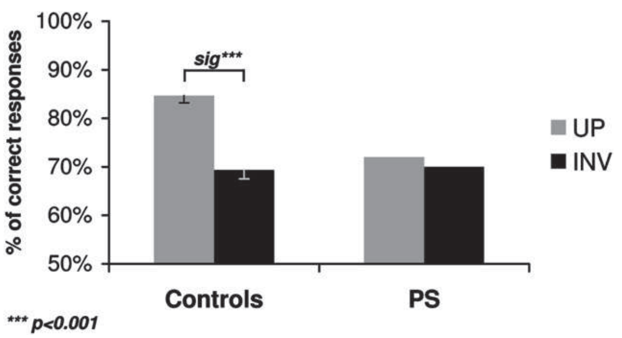

Fig. 2 – Percentages of correct responses of PS and the control participants in Experiment 1. The control participants show a massive FIE, whilst PS does not show any advantage to process the faces when they are upright. Bars represent the standard errors.

3.2. *Experiment 2: delayed matching of faces upright and upside-down*

3.2.1. *Materials and methods*

3.2.1.1. Control participants. Eleven healthy control participants (9 females) were tested (mean age: 57.45; SD: 7.62).

3.2.1.2. Stimuli. Sixteen color faces (8 females) were used, with two sets of photographs for each face (target and probe stimuli were always 2 different full front photographs of the same person). Each photograph was placed in an oval in order to remove the external cues (hair, ears, accessories, ...) (Fig. 3). Each photograph was used in upright and inverted orientation. Stimuli subtended approximately 9.2° in height and 7.1° in width, on a white background.

3.2.1.3. Procedure. The procedure used was an ABX delayed matching task. Each trial began with a white screen (1000 msec), followed by the target (3000 msec), an ISI (2000 msec), and the

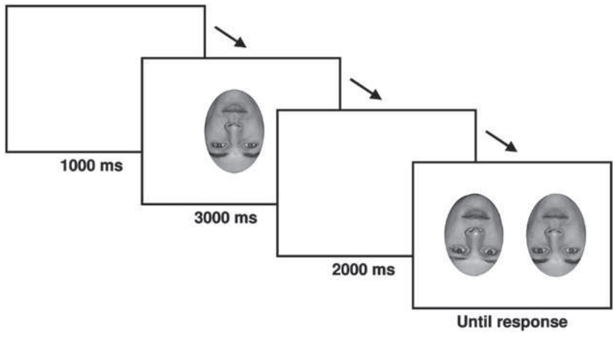

Fig. 3 – Example of trial used in Experiment 2.

probe screen (infinite) (Fig. 3). Each new trial was initiated after the response of the participant. Participants were instructed to select one of the two faces that was the same as the previously shown target, by pressing a keyboard key (left or right) corresponding to the location of the target face. They were asked to be as accurate as possible, and respond as fast as they could. The 32 photographs were used two times in both orientations. The experiment was divided into two blocks of 64 randomized trials and 7 trials were presented as examples (not analyzed). In total, 64 trials were used for both orientations. The experiment was performed two times by the patient PS to ensure reliability of the findings.

3.2.2. *Results*

Control participants performed significantly better for upright than inverted faces (95.3% *vs* 88.4%, $t_{10} = 4.52$, $p < .001$). In comparison to normal controls, PS was impaired both for upright (78.9%, $t = 4.33$, $p < .01$) and inverted faces (77.3%, $t = 2.67$, $p < .05$). Most importantly, she did not present any inversion effect ($t_{254} = .30$, $p = .38$) (Fig. 4A).

Control participants showed a strong FIE in RTs (respectively 1562 msec and 1984 msec for upright and inverted faces; $t_{10} = 4.43$, $p < .001$). Compared to control participants, PS was slowed down for upright (3669 msec, $t = 3.15$, $p < .01$) and inverted faces (3353 msec, $t = 2.43$, $p < .05$). Again, she did not present a FIE ($t_{187} = .86$, $p = .19$) (Fig. 4B).

We also computed an index of inversion effect that combines the accuracy rates and correct RTs, in order to take into account possible speed-accuracy trade-offs and to assess the magnitude of the FIE for PS and each control participant. First, we computed the inverse efficiency (average response times of the correct trials divided by accuracy; Townsend and Ashby, 1983). Next, we calculated the percentage of FIE for each participant using the following formula: (Inverse efficiency Upright − Inverse efficiency Inverted)/(Inverse efficiency Upright + Inverse efficiency Inverted). The results showed that PS had a significantly lower face inversion index (−3.51%) in comparison to the control participants (mean: 16.55%; $t = 2.36$, $p < .05$) (Fig. 4C).

3.2.3. *Discussion*

Normal observers show a strong FIE both in accuracy and correct response times. In contrast, PS is impaired at the task (albeit performing well above chance level), and she does not show any difference between upright and inverted faces, neither in accuracy rates nor in correct RTs. This experiment replicates the finding of Experiment 1 with the BFRT, taking into account the response times for correct responses. The only notable difference was that PS' performance with inverted faces was not equal to the control participants, who were still better than the patient with inverted faces. This issue will be addressed in the General discussion section.

In the next experiment, we aimed at strengthening these results and compare the inversion effect for faces to the effect for a non-face highly familiar category, namely

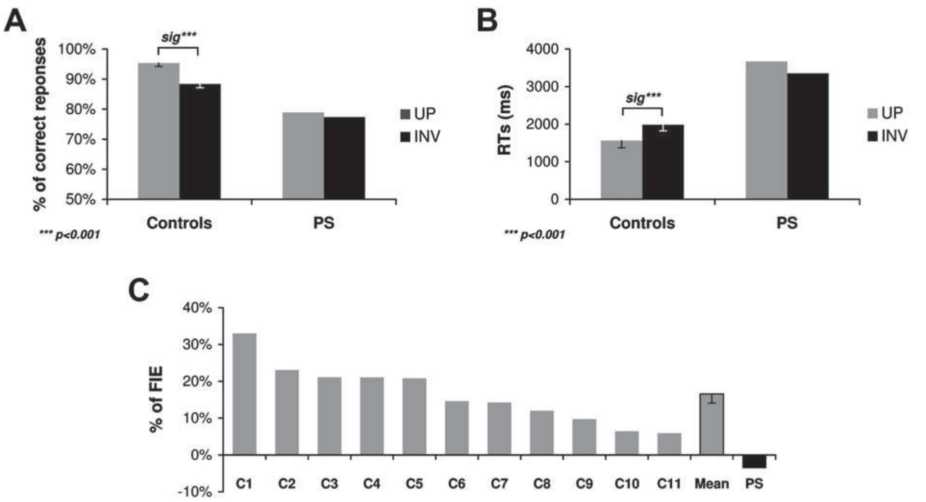

Fig. 4 – Results of PS and the control participants in Experiment 2. A. Accuracy rates (%). The control participants show a massive FIE, whilst PS does not show any advantage for upright faces. B. Average response times on correct trials. Contrary to the controls, PS is not faster in the upright condition in comparison to the inverted condition. C. Magnitude of the FIE for each participant. This measure is based on inverse efficiency scores (average response times of the correct trials divided by accuracy; Townsend and Ashby, 1983). The magnitude of FIE was calculated for each participant using the following formula: (Inverse efficiency Upright − Inverse efficiency Inverted)/(Inverse efficiency Upright + Inverse efficiency Inverted). Bars represent the standard errors.

pictures of cars. It is known that non-face categories also elicit inversion costs in matching or recognition tasks, albeit less strongly than faces (e.g., Yin, 1969; Scapinello and Yarmey, 1970; Valentine and Bruce, 1986; Leder and Carbon, 2006; Robbins and McKone, 2007). The question here was to test whether the patient presents a general abnormal inversion effect that extends to other mono-oriented object categories, or if this peculiar effect is specific to the category of faces.

3.3. *Experiment 3: simultaneous matching of faces and cars upright and upside-down*

3.3.1. *Materials and methods*

3.3.1.1. CONTROL PARTICIPANTS. Nine healthy control participants (6 males) were tested (mean age: 61.89; SD: 7.2).

3.3.1.2. STIMULI. One full front and one 3/4 profile grey scaled photographs of 36 individuals (18 women) and 36 cars were used. The target picture was always a full front picture, and the probe a 3/4 profile picture (Fig. 5). Each photograph was presented in the upright and inverted orientation. The stimuli subtended approximately 7.1° × 5.7° for the faces and 5° × 7.8° for the cars, on a white background. We used pictures of cars to compare to faces because cars are a set of mono-oriented objects, from a highly familiar and visually homogenous category, and they have multiple parts, just like faces (“internal”: lights, radiator grill, window, bumper; “external”: mirrors, wheels, ...). Also, pictures of cars have been used as control stimuli of faces in numerous studies, including Yin (1969)’s seminal study of the FIE.

3.3.1.3. PROCEDURE. We used an ABX simultaneous matching task. Participants had to choose between two 3/4 profile probes located at the bottom of the screen which one was the same than the full front target presented at the top of the screen (Fig. 5). Each trial ended by the response of the participant and was followed by a 1000 msec ISI. Participants were instructed to select one of the two faces or cars that was the same as the previously shown target, by pressing a keyboard key (left or right) corresponding to the location of the target face. Each photograph was presented in both orientations. The experiment was divided into two blocks of 72 randomized trials preceded by 7 practice trials (not analyzed). In total, 72 trials were used for the two orientations (36 per condition).

3.3.2. *Results*

Regarding faces, the control participants presented a strong FIE in accuracy (upright faces: 93.2%, inverted faces: 67.9%; $t_8 = 8.29$, $p < .001$) and in correct response times (upright faces: 3112 msec, inverted faces: 4986 msec; $t_8 = 3.24$, $p < .01$) (Fig. 6A and B). Compared to normal controls, PS was impaired in the upright condition (63.9%; $t = 5.53$, $p < .001$) and she was in the lower range for response times (5339 msec; $t = 1.59$, $p = .075$). With inverted faces, her accuracy was in the normal range (61.1%; $t = .70$, $p = .252$) and she was not significantly slower than controls (6162 msec; $t = .39$, $p = .353$), due to the fact that two normal controls were slower than her in this condition (Fig. 7). She did not present any FIE (accuracy: $t_{70} = .24$, $p = .41$; RTs: $t_{41} = 1.09$, $p = .14$) (Fig. 6A and B; Fig. 7).

For pictures of cars, control participants did not show a significant inversion effect in accuracy (upright cars: 95.1%, inverted cars: 94.1%; $t_8 = 1.00$, $p = .174$) but they did so in RTs (upright cars: 2299 msec, inverted cars: 2633 msec; $t_8 = 3.08$, $p < .01$). PS performed extremely well in the upright cars condition, but not significantly better than controls (97.2%; $t = .52$, $p = .310$). She also obtained a relatively low score in accuracy in the inverted cars condition, so that she was almost below normal range in that condition (88.9%; $t = 1.68$, $p = .065$). Consequently, she had a car inversion effect that was almost significant in accuracy ($t_{70} = 1.39$, $p = .084$). Regarding RTs for cars, PS did not differ from the controls at any orientation (upright cars: 2355 msec, $t = .05$, $p = .482$; inverted cars: 2719 msec, $t = .08$, $p = .471$). Hence, she also

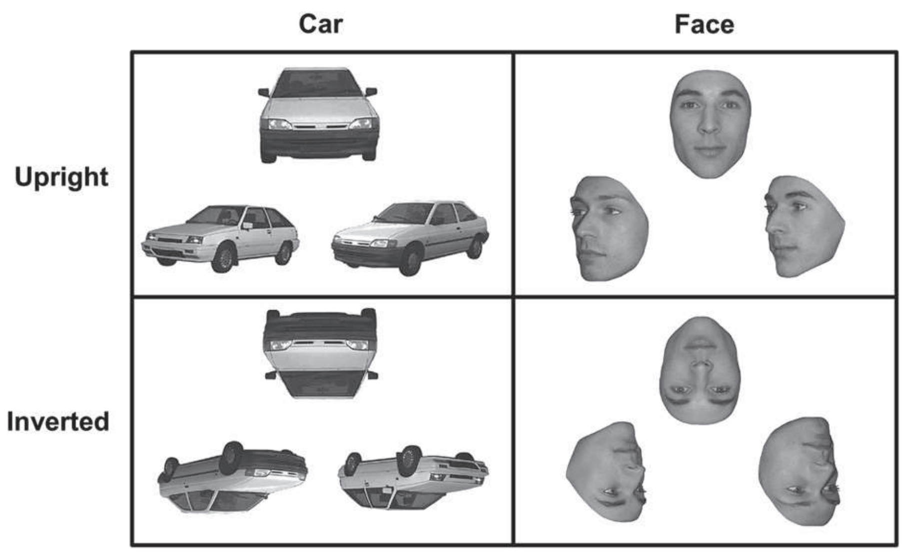

Fig. 5 – The 4 different conditions used in Experiment 3 (simultaneous matching). The same stimuli were also used in Experiment 4 (delayed matching task).

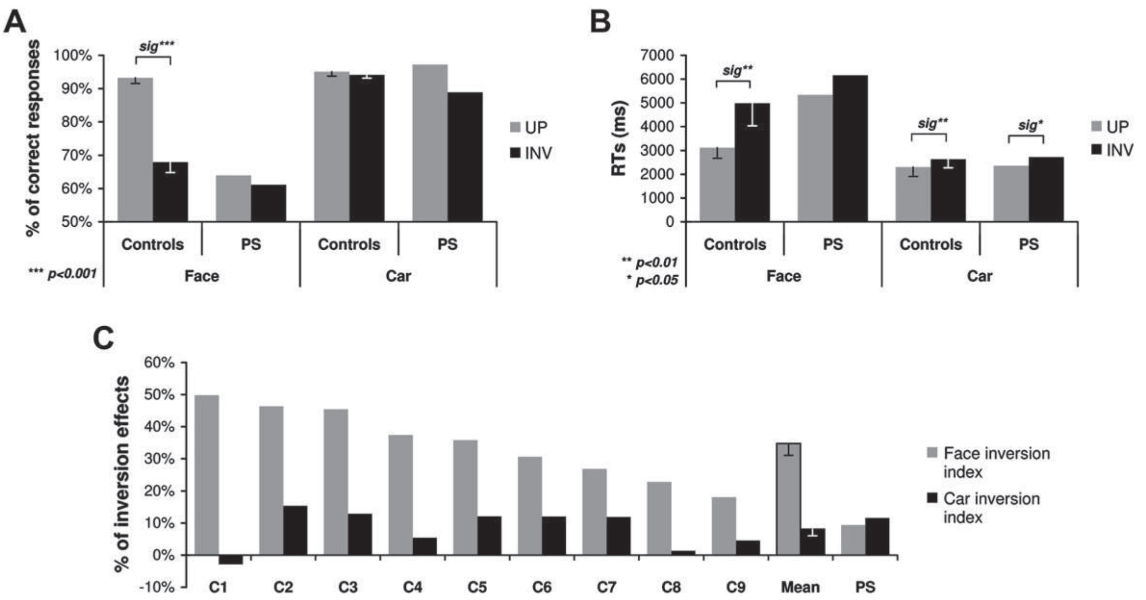

Fig. 6 – Results of PS and control participants in Experiment 3. A. Accuracy rates (%). Controls participants show a strong FIE but no inversion effect for the category of cars. PS does not show a significant effect neither for cars, nor for faces. B. Average response times on correct trials. The controls present a significant effect of inversion in both faces and cars conditions. PS only shows a significant inversion effect for cars. C. Magnitude of the FIE for each participant. In contrast to all of the control participants, PS is the only participant who presents a larger inversion effect for cars than for faces.

presented a significant inversion effect in correct RTs for cars ($t_{61} = 1.81$, $p < .05$) (Fig. 6A and B).

The indexes of inversion effects for faces and cars based on the inverse efficiency (cfr supra) indicate that PS is the only participant who shows a tendency for a larger inversion index for cars than faces (Fig. 6C). In contrast, every single participant presents a larger inversion effect for faces than for cars. Notably, PS' car inversion index is in the normal (upper) range, while her face inversion index is clearly abnormal ($t = 2.17$, $p < .05$).

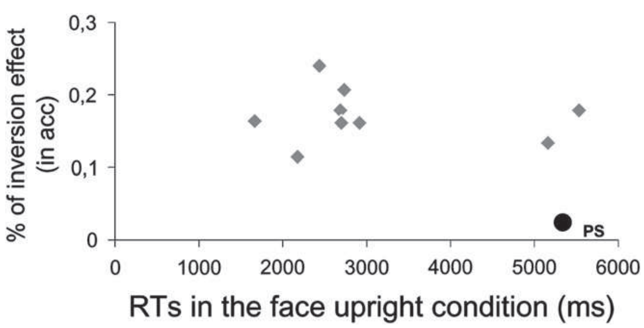

Fig. 7 – Magnitude of the inversion effect in accuracy as a function of speed for the upright face condition of Experiment 3. Each control participant is represented by a grey diamond. While 7 participants were faster than PS, two control participants were as slow as PS to respond. Importantly, these normal participants presented an inversion effect which was as large as the faster controls. The magnitude of the inversion effect was unrelated to the speed of the participants at upright orientation (linear regression analysis: $F_{(1,8)} = .126$, $p = .37$).

3.3.3. *Discussion*

PS has a response profile that is comparable to the normal observers when matching pictures of cars across viewpoint changes. In contrast, she behaves completely differently than these controls when she has to process faces. This demonstrates once again the high selectivity of her impairment for faces, which cannot be attributed to a general difficulty of visual discrimination, even when having to match exemplars of a visually homogenous category across viewpoint changes (Rossion et al., 2003; Schiltz et al., 2006). Regarding the interest of the present study, PS does not present an effect of inversion for faces, in line with the two previous experiments reported. This absence of effect cannot be explained by a general absence of costs of performance following inversion since, if anything, she presented a normal inversion effect for photographs of cars. Thus, these data support the view that the particularly large FIE observed in normal viewers when individualizing faces is not present at all for the acquired prosopagnosic patient PS. In the next experiment, we used the exact same stimuli, this time during a delayed matching task, to reinforce these observations.

3.4. *Experiment 4: delayed matching of faces and cars upright and upside-down*

3.4.1. *Materials and methods*

3.4.1.1. Control participants. Twelve healthy control participants (9 females) were selected (mean age: 58; SD: 7.51).

3.4.1.2. Stimuli and procedure. The stimuli were the same as those in the previous experiment. The procedure was identical to the previous experiment, but for the delay between probe and target items. Each trial began with a white screen (1000 msec), following by the target (2000 msec), an ISI (1000 msec), and the probe screen (infinite). Each new trial was initiated after the response of the participant.

3.4.2. Results

For faces, control participants obtained again a massive inversion effect in accuracy (upright faces: 89.9%, inverted faces: 72.9%; $t_{11} = 9.7$, $p < .001$) and in RTs (upright faces: 1811 msec, inverted faces: 2230 msec; $t_{11} = 6.93$, $p < .001$).

PS obtained low scores in accuracy in the upright condition, even though the difference with normal controls was only marginally significant (73%; $t = 1.37$, $p = .099$). She was significantly slowed down for upright faces relative to controls (4193 msec; $t = 4.44$, $p < .01$). For inverted faces, she obtained similar results as the control participants in accuracy (75%; $t = .19$, $p = .426$) but she was also slowed down (4290 msec; $t = 3.63$, $p < .01$) (Fig. 8A and B). Again, contrary to normal controls, PS showed no FIE, neither in accuracy ($t_{67} = .19$, $p = .426$), nor in response times ($t_{46} = .19$, $p = .426$).

Regarding pictures of cars, the controls showed the exactly same profile than in the previous experiment: no inversion effect in accuracy (upright cars: 95.2%, inverted cars: 94.1%; $t_{11} = .636$, $p = .269$) but a significant inversion effect in correct response times (upright cars: 1612 msec, inverted cars: 1776 msec; $t_{11} = 3.74$, $p < .01$). PS was as accurate as normal controls for the upright cars condition (92.1%; $t = .65$, $p = .265$) and for the inverted condition (91.9%; $t = .41$, $p = .344$). Similarly to the controls, her car inversion effect was not significant ($t_{73} = .034$, $p = .487$). On the other hand, PS' response times were significantly longer than the controls in both conditions (upright cars: 3317 msec, $t = 2.49$, $p < .05$; inverted cars: 3585 msec, $t = 2.38$, $p < .05$) but she did not present a significant car inversion effect ($t_{62} = .66$, $p = .255$) (Fig. 8B). Thus, the only difference between the results of this experiment and the previous one is that PS was slowed down at responding for car pictures relative to controls.

Finally, the indexes of inversion effects calculated for faces and cars on the basis of the inverse efficiency show that, as in the previous experiment, PS obtained a larger (although not significant) inversion index for cars than for faces (Fig. 8C). Again, PS is the only participant to present such a profile, all the controls showing a disproportionate larger inversion effect for faces than for cars. As in the previous experiment, PS' s car inversion index is in the normal range, while her face inversion index is close to zero, and thus clearly abnormal ($t = 3.02$, $p < .01$).

3.4.3. Discussion

Overall, this fourth experiment replicates the conclusions of the three previous experiments and show that PS presents a profile that is extremely different from the control participants concerning face processing only: her FIE is completely inexistent, and this effect cannot be accounted for by a general factor related to the orientation of the stimulus. Here, for pictures of cars, she was as accurate as normal controls, but she was significantly slower, whether the stimuli were presented upright or upside-down. Such response delays were observed for PS previously in some tasks for non-face objects (Rossion et al., 2003), but contrary to what is found for faces, they are not consistent and do not appear to be related to the object category (e.g., pictures of cars were responded as fast as controls in Experiment 3), the presentation mode (delayed or simultaneous presentation, see Rossion et al., 2003; Schiltz et al., 2006), or the change of viewpoint between

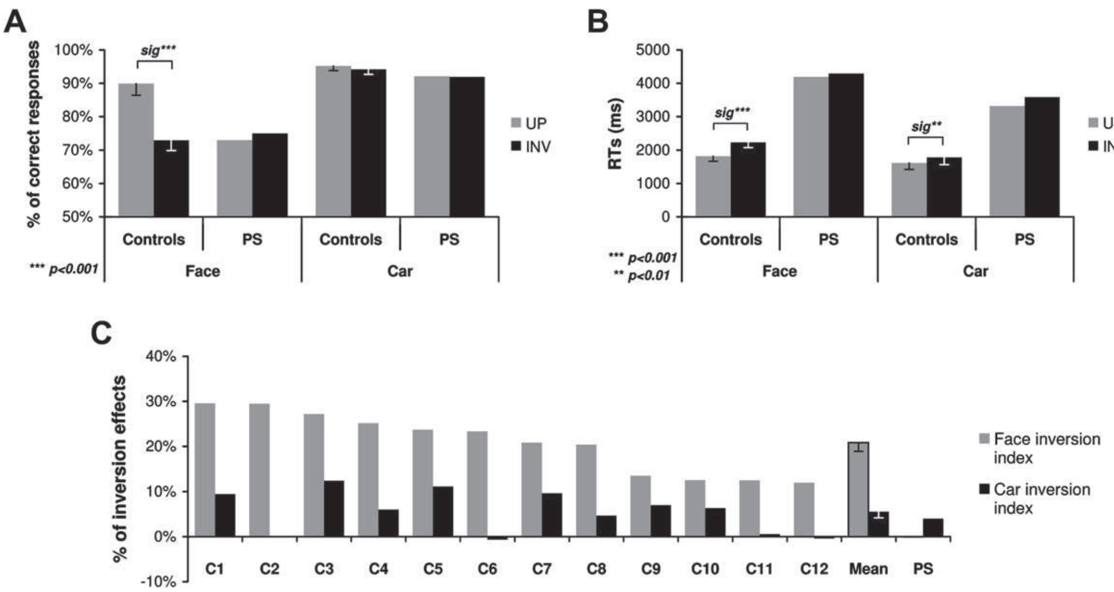

Fig. 8 – Results of PS and the control participants in Experiment 4 (delayed matching of faces or cars). A. Accuracy rates (%). Normal controls show a significant inversion effect for faces but not for cars. PS does not show a significant inversion effects, neither for faces, nor for cars. B. Average response times on correct trials. Control participants obtained significant inversion effects for both cars and faces, whilst PS does not show any significant inversion effect. C. Magnitude of the Face and Car Inversion Effect for each participant. As in Experiment 3, PS obtained a larger inversion effect for cars than for faces, and she did not differ from normal controls for pictures of cars, but did so for faces.

target and probe item (which was identical in Experiments 3 and 4). Given this inconsistency and the excellent performance with non-face objects, in contrast to faces, we attribute these observations to the patient's being particularly conservative in taking her decision in certain tasks.

In our final experiment, we aimed to replicate our observations in a familiar face recognition task, with a large set of personally familiar faces.

3.5. Experiment 5: familiarity judgment with upright and inverted faces

The patient PS is not only a particularly interesting patient for her deficit restricted to the category of faces and her pattern of occipito-temporal lesions sparing the right middle fusiform gyrus ('fusiform face area', 'FFA', see Rossion et al., 2003; Sorger et al., 2007), but also because of her excellent memory and ability to perform complex tasks for long durations, as well as her active social and professional life. In this experiment, 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 color, etc. Yet, when the set of stimuli is not mixed with unfamiliar faces, her recognition from static full photographs of the children is quite good, and still well above chance level for cropped faces revealing only internal features (Orban de Xivry et al., 2008). Here we used this opportunity to characterize PS' inversion effect during a familiarity decision 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. This is 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 is roughly equal with the different faces, which would not be the case if we used 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. To our knowledge, this is the first investigation of personally familiar face recognition in AP across the two orientations.

3.5.1. Materials and methods

3.5.1.1. Control participants. To assess the effect of inversion in the task and with these stimuli, we tested PS' only two female colleagues of the kindergarten, C1 (60 years old) and C2 (24 years old). Both of them had no history of neurological or vascular disease, head injury, alcohol abuse, or cognitive complaints.

3.5.1.2. Stimuli. The stimuli used in the experiment were a set a 26 photographs of familiar faces and 26 photographs of unfamiliar faces. The familiar faces consisted in the pictures of the 26 children from 3 to 4 years-old belonging to the classroom of PS. The unfamiliar faces were photographs of unknown children of the same gender, age and ethnical origin. The photographs were colored pictures and were placed in an oval in order to remove the external cues (hair, ears, accessories, ...). Each photograph was used in upright and inverted orientation. The stimuli subtended approximately 6.4° in height and 5.7° in width, on a white background.

3.5.1.3. Procedure. The procedure used here was a familiarity task. The participants had to decide for each picture if the face was familiar or not ("a child belonging to the kindergarten"). Each trial began with a central black cross (1500 msec), following by an ISI (250 msec) and the target (infinite). Each new trial was initiated after the response of the subject. PS and the two controls were instructed to decide for each picture presented if the face was familiar (i.e., from the kindergarten) or not by pressing a corresponding key (right for familiar, left for unfamiliar). They were asked to be as accurate as possible, and respond as fast as they could. The 26 photographs of familiar and unfamiliar faces were used in both orientations. The experiment was presented as a single block of 104 randomized trials. In total, 52 trials were used for each orientation (26 per condition).

3.5.2. Results

The two control participants (C1 and C2) were very accurate to judge the familiarity of the children faces in the upright condition (respectively 94% and 96% of correct responses), but their scores were much lower in the inverted condition (respectively 60% and 67%) (Fig. 9A). Consequently, both of them obtained a very strong FIE, significant at the single-subject level (C1: $t_{102} = 4.55$, $p < .001$; C2: $t_{102} = 4.06$, $p < .001$). The d' scores also show a strong advantage for upright faces (C1: 3.75 for upright faces, .97 for inverted faces; C2: 3.19 for upright faces, .49 for inverted faces). This FIE was confirmed in the analysis of correct response times: C1 and C2 were significantly faster in the upright condition (C1: $t_{73} = 1.81$, $p < .05$; C2: $t_{78} = 2.34$, $p < .05$) (Fig. 9B).

PS obtained very low scores on accuracy both for the upright condition and the inverted condition (respectively 60% and 52%; no significant inversion effect, $t_{102} = .78$, $p = .218$). She detected more familiar faces in the upright than in the inverted orientation (11/26 *vs* 4/26), but she also presented more false alarms in the upright condition (6/26 *vs* 3/26), leading to very low d' scores (d' of .54 and .18, respectively). Similarly, in correct response times PS did not show any difference between upright and inverted faces ($t_{54} = .68$, $p = .249$).

3.5.3. Discussion

During familiarity decisions on personally familiar faces, we found highly significant effects of face inversion at the single-subject level (about 30% decrease of performance). In contrast, PS did not show an advantage at recognizing faces of the

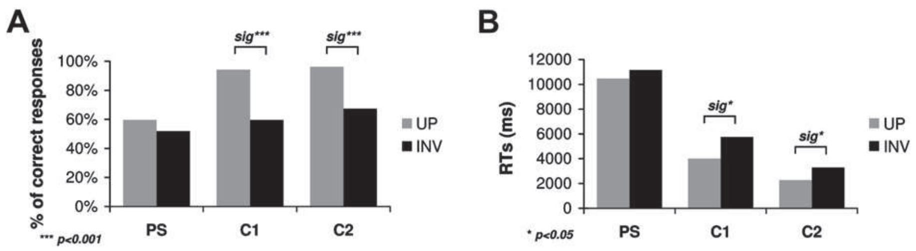

Fig. 9 – Results of PS and the control participants in Experiment 5 (familiarity decision). A. Accuracy rates (%). C1 and C2 show a strong FIE, whilst PS does not show any effect. B. Average response times on correct trials. C1 and C2 also present, contrary to PS, a significant FIE in response times.

children she is used to see every day when they were presented in the classical upright orientation as compared to when the pictures were inverted. Overall, one is struck by the particularly low performance of the patient PS, both with upright and inverted faces, as compared to the previous 4 experiments. However, this is not particularly surprising: even with unlimited presentation duration, this task in which familiar and unfamiliar faces are mixed is extremely difficult for a prosopagnosic patient. Rather than comparing two unfamiliar presented faces in detail, PS has to compare the displayed picture with a series of mnesic representations of faces (to decide whether the depicted face is familiar or not). She is faced with a very complex problem, closer to her real life difficulties, and fully revealing the extent of her prosopagnosia. The major point and interest of this experiment here is that while this task leads to huge inversion effects in single normal subjects, there was no such effect at all for the patient PS: she was neither able to take advantage of the normal orientation of the faces, nor did she perform better with inverted faces.

4. General discussion

The objective of this study was to clarify how AP affects the processing of upright and inverted faces, in order to shed light both on the nature of the prosopagnosic impairment and the FIE. For the first time to our knowledge, this question was investigated here in depth with a case of AP who is not impaired at object recognition and discrimination of individual exemplars of non-face object categories (Rossion et al., 2003; Schiltz et al., 2006), a fact that was also supported in the present study (Experiments 3 and 4). Most importantly, the strengths of the present study also lie in the consistency of observations made in 5 different experiments, varying the stimuli and the presentation conditions (delayed or simultaneous matching, with or without change of viewing conditions), ruling out general effects of orientation, and taking into account both accuracy and response times to consider any possible speed-accuracy trade-off and obtain a global measure of the FIE for each individual participant. PS' performance with upright and inverted faces was also compared to carefully selected normal controls. For these reasons, we would like to argue that the present report is, to the best of our knowledge, the most complete and systematic investigation of the FIE in AP to date. From the first to the last experiment, PS did not show any advantage at processing upright as compared to inverted faces. She never presented significant FIEs, neither on accuracy, nor on response times, whilst the control participants showed very strong effects in all experiments. Even though she was, obviously, not as accurate and as fast as normal participants for upright faces, PS also performed well above chance level in these experiments, ruling out a lack of FIE being due to floor effects. Moreover, comparing the category of faces to another category of mono-oriented stimuli, PS was the only participant who presented a smaller effect for faces. Finally, also for the first time in the literature, these results were found in a recognition task with highly familiar faces, for which extremely large effects of inversion can be found in single observers (Experiment 5).

With respect to the data of the present study, two relatively small issues are worth mentioning here. First, we note that when the faces were presented upside-down, the normal controls still performed slightly better than the patient PS in some but not all experiments. This was the case in Experiment 2 (accuracy rates and RTs), Experiment 4 (RTs) and for the familiarity decision task in Experiment 5 (accuracy and RTs). However, this was not the case in Experiments 1 and 3. Thus, our data cannot lead us to conclude that PS' processing of an inverted face is perfectly normal. These observations may suggest that expert (holistic) face processes are not completely abolished by inversion (Murray, 2004; Rossion and Boremanse, 2008). Alternatively, we cannot exclude that there may be some additional general factors worsening the impaired face processing of the prosopagnosic patient PS, making her performance with inverted faces slightly below normal range (e.g., lower normal range for color perception, small paracentral left scotoma, visual acuity slightly below normal range, see Sorger et al., 2007). Importantly, these factors were at play for faces (and cars) presented at both orientations, and cannot account for the main findings of the present study: the lack of inversion effect for the patient PS.

Second, one may wonder if the patient's lack of FIE could be due to her slowing down at processing faces in general. Of course, since it reflects a lack of expert face processing, the slowing down of the patient at matching or recognizing faces at upright orientation somehow *has to* be related to the absence of inversion effect: she has to rely on unusual strategies to individualize faces, these are costly in time, and they do not appear to be affected by inversion. However, it is not the slowing down *per se* which accounts for the absence of FIE in this patient, at least for two reasons. First, the magnitude of the FIE was unrelated to the speed of normal participants in these experiments. In fact, some control participants were also particularly slow, but showed a large inversion effect. For instance, in Experiment 3, the control participant C1 was even slower than PS at upright orientation (5534 msec *vs* 5339 msec). However, while this control participant took more than twice that time to do the same task with inverted faces (11254 msec), PS showed only a small, non-significant, increase of response times (6162 msec). In general, the magnitude of the inversion effect as computed in accuracy rates or correct RTs was unrelated to the speed of the participants at upright orientation, as we illustrated in Experiment 3 (Fig. 7). Second, there is evidence for clear inversion effects in memory for faces (old/new discrimination tasks) or face matching tasks in normal children (e.g., Mondloch et al., 2002) for instance, despite the fact that children are notoriously much slower than adults, and do not perform at ceiling in these tasks (see Crookes and McKone, 2009).

Overall, these observations lead to the conclusion that the inversion effect is abnormal for the prosopagnosic patient PS, being in fact completely cancelled out: the patient is no longer better and/or faster at individualizing upright than inverted faces. However, and importantly, we would like to stress out that, across our five experiments, there was no evidence whatsoever that PS performed better with inverted than upright faces. As indicated in the introduction, such a reversal of the inversion effect has been previously observed clearly in only two cases of AP [LH (Farah et al., 1995a, 1995b; de Gelder and Rouw, 2000a) and AD (de Gelder et al., 1998)]. While this idea that prosopagnosic patients perform generally better with inverted faces remains quite influential in the field, this view is in fact not supported by the bulk of the evidence. Precisely, before discussing the theoretical implications of the present findings, how do they compare with the existing literature on AP and face inversion?

4.1. *The absence of FIE in prosopagnosia*

As indicated in the introduction, several prosopagnosic patients generally tested in a single experiment showed an absence of inversion effect (one case in McNeil and Warrington, 1991; Boutsen and Humphreys, 2002; Delvenne et al., 2004), compatible with the present findings. Also mentioned in the introduction, several other cases present an ambiguous pattern of results with respect to processing upright and inverted faces: the patients CR, SM and RN, reported in several studies (Gauthier et al., 1999; Marotta et al., 2002; Behrmann et al., 2005). However, considering these 3 latter studies altogether and both accuracy rates and correct RTs, it is clear that these 3 prosopagnosic patients do not present a normal FIE, and one would rather conclude that their FIE is strongly reduced or even abolished compared to normal observers. A reduced inversion effect was also observed for a recently described case of prosopagnosia with no object recognition impairment, albeit in a complex whole versus part matching task (Riddoch et al., 2008). All these reports indicate an absence of FIE in prosopagnosia and are compatible with the present observations, even though the data of these previous studies were usually obtained in a single experiment, and without a full and systematic investigation of upright and inverted face processing as carried out in the present study.

To our knowledge, only two cases of prosopagnosia have been reported in the literature with a significant advantage at processing upright as compared to inverted faces. In the first report (Bukach et al., 2006), the patient LR showed a normal inversion effect when the mouth was diagnostic for discriminating faces, but it was reduced or abolished when faces differed at the level of the eyes. Thus, his overall FIE was weaker than in normal controls, albeit not fully abolished. This observation is in agreement with an abnormally reduced FIE in prosopagnosia, but would deserve further investigation. In contrast, the recently described patient DBO showed a completely normal inversion effect, both in accuracy rates and RTs during individual face discrimination (Anaki et al., 2007). However, this patient had unilateral damage to the left occipito-temporal cortex and presented a rather unusual neuropsychological profile compared to other cases of prosopagnosia. Strictly speaking, he was defined as a case of AP because of his impairment in famous face recognition. However, he was impaired at identifying all kinds of familiar nonface items presented visually, on top of his inability to recognize visually presented words. He also presented great difficulties at associating semantically related objects, and general (visual and verbal) memory impairments. Hence, he should rather be referred to as a case of general semantic agnosia (Riddoch and Humphreys, 1987) rather than prosopagnosia. Importantly, contrary to all cases of prosopagnosia referred to above, this patient was perfectly able to match (upright) faces, at normal speed. In the same vein, a normal inversion effect can be observed in patients who are unable to identify faces and objects following right anterior fronto-temporal dementia with predominant– but not exclusive– symptoms in the visual modality, but who have normal unfamiliar upright face matching (Busigny et al., 2009). This indicates that patients with general semantic memory impairments prevalent in the visual modality may not present the reduced/abolished inversion effect which characterizes classical acquired prosopagnosic patients. This pattern would be observed only if matching of unfamiliar upright faces is at least below normal range in accuracy and/or speed, as in the vast majority of cases.

In summary, the present observations and an overview of the literature indicate that prosopagnosic patients who are impaired at matching upright individual faces do not show a further decrease of performance when faces are inverted, or at least to a lesser extent than normal observers. Importantly, we showed here with the experiments carried out on PS that this abnormal FIE is not due to chance level performance for upright faces or floor effects, that it is specific to faces, concerns both accuracy rates and correct RTs, and is observed for both unfamiliar and familiar faces.

4.2. *FIE and prosopagnosia: loss of holistic processing*

Why is the FIE reduced or abolished following prosopagnosia, and what does this tell us about the nature of the face impairment of these patients? Behavioral, electrophysiological and neuroimaging studies indicate that the locus of the FIE is at perceptual encoding (Farah et al., 1998; Freire et al., 2000; Jacques et al., 2007; Jacques and Rossion, 2007; Mazard et al., 2006; Yovel and Kanwisher, 2005), which is in line with the fact that all prosopagnosic patients present impairments at perceptual face processes (Farah, 1990; Davidoff and Landis, 1990; Delvenne et al., 2004). While the nature of the diagnostic cues for individualizing faces that are more or less affected by face inversion is still a matter of debate (e.g., shape *vs* texture, Russell et al., 2007; mouth *vs* eyes, Barton et al., 2001; relative distances between features *vs* local details, Freire et al., 2000; vertical *vs* horizontal distances between features, Goffaux and Rossion, 2007; Sekunova and Barton, 2008), most authors agree that a primary cause of the FIE is the loss of the ability to perceive a face holistically (Farah et al., 1995b; Rossion, 2008). That is, inversion prevents the ability of the face processing system to *integrate simultaneously the multiple features of a face into a unified perceptual representation*. This view is supported by evidence that the interdependence among facial features for upright faces is strongly affected by inversion (Sergent, 1984; Tanaka and Farah, 1993; Tanaka and Sengco, 1997; Young et al., 1987; Rossion and Boremanse, 2008).

Consequently, the absence of FIE following prosopagnosia does not only reinforce the view that these patients do not process faces holistically: it strongly suggests that this problem is at the heart of their face processing impairment. As indicated briefly in the introduction, there is wide evidence in the literature that brain-damaged prosopagnosic patients suffer from an inability to perceive faces holistically, a rather old proposal inspired by the Gestaltist view of perception (Galli, 1964). For instance, Levine and Calvanio (1989) defined the prosopagnosic patient LH as being unable to "*get an overview of an item as a whole in a single glance*". Rather, LH was described as using a sequential visuospatial processing, attending to single features. Similarly, Sergent and Signoret (1992) described one of their prosopagnosic patient as unable "*to process the internal facial features and their relationships, which precluded a reliable extraction of the physiognomic invariants*". Saumier et al. (2001) also interpret the deficit of their prosopagnosic patient as the "*incapacity to process multiple face part information into integrated visual wholes*" (see also Boutsen and Humphreys, 2002). In all these cases, the patients were tested with various paradigms measuring the integration between facial features, and showed abnormal patterns of performance. In line with these observations, we have collected independent evidence of the patient PS, showing that she has also lost her ability to process faces holistically: she presents no composite and whole-part face effects and has to focus exactly on each feature (mouth, right or left eyeball) when identifying a face (Orban de Xivry et al., 2008) rather than fixating the upper middle part of the face, as normal observers do (Hsiao and Cottrell, 2008).

Taken altogether, these observations suggest that AP is generally characterized by an inability to process individual faces holistically, leading to a loss of the advantage at processing the face when it is presented in its normal upright orientation. When the face is presented upside-down, normal observers cannot rely on holistic processes anymore, resorting to an analytical approach that is costly in time and leads to inaccurate responses (e.g., Sergent, 1984; Tanaka and Farah, 1993). However, this manipulation does not affect further a brain-damaged patient who is already unable to process an upright face holistically. Thus, the lack of FIE in AP is an important observation because it indicates that the expert faces processes that are damaged following brain lesions causing prosopagnosia are specific to the upright face orientation and that the deficit of these patients lies primarily in the inability to process the individual face as a holistic representation.

4.3. *Generalization of face inversion impairments and the issue of developmental prosopagnosia*

The present observations are largely in agreement with the literature, and indicate that acquired prosopagnosic patients generally show an absence of inversion costs when having to individualize faces. However, importantly, we do not claim on the basis of the results obtained here and our review of the literature that *all* cases of prosopagnosia would not present any inversion effect at all in any given experiment. First of all, we have shown an absence of inversion effect during the processing of individual faces (i.e., identity judgments), not during other face categorization tasks. It may well be that inversion affects the detection of a face in a visual scene, facial expression, age or gender categorization in prosopagnosic patients who are not impaired at these tasks, just as it does for normal observers (e.g., Purcell and Stewart, 1988; McKelvie, 1995; Santos and Young, 2008). As a matter of fact, the patient PS is able to categorize upright and inverted Mooney stimuli as faces and nonfaces respectively (Dricot et al., 2008). Her ability to categorize facial expressions is relatively well preserved as well (Rossion et al., 2003) so that she may present a normal inversion effect for categorizing facial expressions.

Second, even during individual face matching tasks, it may be that a relatively weak advantage at processing upright over inverted faces is found in some patients who do not process faces holistically, insofar as inversion affects also the processing of local facial features, or parts (nose, mouth, eyes, ...), even when they are isolated from the whole face (Rakover and Teucher, 1997; Bartlett et al., 2003).

Third, our findings and review only concern cases of prosopagnosia following brain damage in adulthood, i.e., people who presumably developed a normal face recognition system prior to their lesion. A number of patients presenting important lifelong impairment in face recognition, and referred to as cases of congenital (or developmental) prosopagnosia (CP) have been reported in the literature, in particular over recent years (for a review see Behrmann and Avidan, 2005). These subjects do not report any injury and do not show visible brain damage as in cases of AP, but anatomical abnormalities have been observed at least in some cases (significantly smaller anterior fusiform gyrus and/or reduced white-matter fibers in ventral occipito-temporal cortex, Behrmann et al., 2007; Thomas et al., 2009). With respect to face inversion in cases of CP, the data are also mixed. Some studies report an *absence of inversion cost* (Nunn et al., 2001, patient EP in accuracy; Duchaine et al., 2006, patient Edward in accuracy and RTs). One study reports the case of a patient with a *reduced FIE* (de Gelder and Rouw, 2000c, patient AV in accuracy and RTs). Another study on a group of four CPs (Righart and de Gelder, 2007) also shows a reduced FIE in two patients (HV and JS in accuracy and RTs), but a normal effect in the other two (GR in RTs and

CB in accuracy and RTs). As for AP, the same patients are also sometimes reported with different patterns. The patient RP was first reported as presenting a *reverted inversion effect* in accuracy and RTs (de Gelder and Rouw, 2000c), but this patient was reported latter without any significant inversion effect, neither in accuracy, nor in RTs (Rouw and de Gelder, 2002). Behrmann et al. (2005) tested 5 developmental prosopagnosic patients (TM, KM, NI, MT and BE). Considered as a group, the patients were reported to be slightly faster with inverted faces. However, it was not the case for each of them individually (KM for example was clearly faster for upright faces) and four of them did not show any inversion effect (neither normal, nor reverted) in term of accuracy.

Thus, overall, the outcome of inversion on individual face processing in CP remains largely unclear. This may also be due to different paradigms used, but more likely reflect the fact that the definitions and criteria used to classify normal observers as presenting congenital prosopagnosia are not uniform at all across studies. We also note that the nature of the impairment for cases of AP as described here and subjects characterized with CP does not seem to be equivalent. For instance, cases of CP generally have impairments in visual recognition which extend largely beyond faces (Behrmann et al., 2005), compatible with their reduced white-matter fibers in ventral occipito-temporal cortices important for general shape recognition (Thomas et al., 2009).

4.4. *Inversion superiority in AP: a visual field defect explanation?*

In an influential study, the patient LH has been reported at performing better with inverted than upright faces (Farah et al., 1995a, 1995b), an observation replicated later with the same patient (de Gelder and Rouw, 2000b). However, in light of the review of the literature above, there appear to be strong doubts about the validity and generalizability of this paradoxical reverted inversion effect in prosopagnosia, which seems to be the exception rather than the rule. Moreover, the rather far-stretched interpretation of the authors that this paradoxical reverted inversion effect was due to a "*negative interference of a malfunctioning holistic processor when the face is presented upright, preventing the patient to use the feature-by-feature processing he employs for inverted faces*" (Farah et al., 1995a, 1995b) is highly unlikely. This is a rather complex high-level visual account of a patient's performance, which makes at least two unwarranted assumptions: (1) that holistic processes can be only partly but not fully impaired in these patients, and most importantly (2) that these residual processes do not help the patient but rather interfere with the feature-by-feature analysis of the face. The lower performance of prosopagnosic patients in processing whole faces that differ by a part as opposed to their processing of the isolated face part has sometimes been used as a support for the second assumption ("interference effect", e.g., de Gelder and Rouw, 2000b; Boutsen and Humphreys, 2002; Riddoch et al., 2008). However, we would like to argue that there is no need to call upon a putative "interference" between holistic and analytic (part-based) processes to account for such observations. According to a much simpler account, the advantage at processing face parts relative to whole faces observed with such patients (e.g., Delvenne et al., 2004) is due to a loss of the ability to process faces holistically, without any interference factor at play. Indeed, a primary advantage of normal holistic face processing is that it allows identifying rapidly and efficiently the location and nature of the diagnostic cues to individualize faces, i.e., to resolve ambiguity. The face is seen as a whole at once, so there is no need to analyze each feature in turn. If this process is impaired, the patient does not know which feature is diagnostic in a whole face and the task is difficult. However, if a single part is presented rather that the whole face, the experimenter has done the selection process for the patient. Hence, prosopagnosic patients, including PS, perform much better and faster for single isolated parts that whole faces (de Gelder and Rouw, 2000b; Boutsen and Humphreys, 2002; Delvenne et al., 2004; Riddoch et al., 2008) yet there is no need to interpret this observation as resulting from a putative interference effect (of the whole face on the parts). Supporting this view, even when whole faces are presented, these patients also improve their performance dramatically when there is no ambiguity as to which feature of the face is diagnostic (Barton et al., 2002; Joubert et al., 2003; Delvenne et al., 2004; Ramon and Rossion, 2010).

If inversion superiority in AP is rare and unlikely to be caused by interference effects, how can one then account for such observations? One difficulty that may arise when comparing upright and inverted individual face processing in brain-damaged patients is that if there is no difference of difficulty of processing between the two orientations, another impairment – unrelated to face processing – may tilt the balance of observations in one direction or another. One basic principle of science, which should typically apply to Neuropsychology, suggests that one should never seek to explain a psychological fact by a mechanism at a higher level if it can be explained by one at a lower level (Morgan, 1894). Here, the rare studies that reported a relative advantage at processing inverted faces in prosopagnosia did not consider a much simpler, low-level, explanation of this phenomenon: acquired prosopagnosic patients generally suffer from large loss of sensitivity in the upper visual field, in particular in the left side (Hécaen and Anguerlergues, 1962; Meadows, 1974; Bouvier and Engel, 2006). These visual field defects can be explained by the fact that prosopagnosia is generally caused by posterior ventral lesions extending to early visual areas (e.g., Damasio et al., 1982; Barton et al., 2002; Sorger et al., 2007). Moreover, since the optic radiations carrying information coming from the upper part of the visual field run in the depth of the temporal lobe, even lesions rostral to V1, but affecting the white matter of the temporal lobe, may lead to upper visual field defects (Levin, 1999; Nilsson et al., 2004; Yogarajah et al., 2009). More precisely, a superior homonymous quadrantic defect can be the consequence of damage to the inferior fibers of the optic tract, the optic radiation in the temporal lobe, or in the inferior occipital cortex (Levin, 1999).

Interestingly, the two visual agnosic patients who have been reported as having a clear superiority for processing faces presented upside-down were characterized by such upper visual field defects. This is particularly the case for the patient LH, who has important upper visual field defects (Levine and Calvanio, 1989). In the experiments in which a superiority for inverted stimuli was found (Farah et al., 1995a, 1995b; de Gelder and Rouw, 2000a), the stimuli were presented for limited durations. Hence, LH may have found it easier to answer when more local details at the level of the eyes and eyebrows were readily available to him in the inverted orientation. Interestingly, when stimuli were presented for a longer time, LH did not longer show this significant advantage at processing inverted faces (Experiment 4 in Farah et al., 1995a, 1995b). Most importantly, LH showed the exact same advantage for inverted pictures of non-face objects (shoes; de Gelder and Rouw, 2000a), for which diagnostic local information is located in the upper part of the stimulus. Given that pictures of shoes do not even lead to inversion costs for normal observers (de Gelder et al., 1998) and are not known to be processed holistically, it is very unlikely that a high-level explanation – i.e., malfunctioning holistic processor for pictures of shoes interfering with analytical processes – could account for this finding. Rather, the patient may have simply been able to perform better with inverted pictures due to his upper visual field defect and the fact that most diagnostic features are located in the superior area of such stimuli.

The other patient who presented a clear advantage at processing inverted faces (AD, de Gelder et al., 1998) in accuracy (no RTs reported) had bilateral occipito-temporal lesions, leading to visual agnosia, achromatopsia and pure alexia in addition to her severe prosopagnosia. Even though this patient was reported with largely normal upper visual fields (Bartolomeo et al., 1998), Goldman perimetry also showed a large paracentral scotoma which concerned almost exclusively the upper visual field in central vision (up to 4° in the left, more than 10° in the right, see Figure 2 in Bartolomeo et al., 1998). Furthermore, identical observations as for LH were made with this patient on non-face objects, the patient AD showing a reverted inversion effect with pictures of shoes (de Gelder et al., 1998). Since the size of the stimuli was not reported in that study, we do not know if the upper visual field scotoma of AD covered the top part of faces and shoes pictures which were presented to the patient, but this is likely.

In summary, the common belief in the face processing literature that acquired prosopagnosic patients perform better with inverted than upright faces (Farah et al., 1995a, 1995b; de Gelder and Rouw, 2000a, 2000b) is not justified because such cases are the exception rather than the norm, and they all present impairments in recognizing visual forms and upper visual field defects. Most importantly, the view that such an advantage at processing inverted faces in AP patients would be due to an interference of malfunctioning holistic processor over part-based processes (Farah et al., 1995a, 1995b) is probably incorrect.

Rather, we suggest that paradoxical inversion superiority in prosopagnosia may reflect nothing more than the effect of a low-level visual impairment superimposed on an equal processing of upright and inverted faces by high-level face processes. If anything, these observations reinforce again the interest of testing single cases of prosopagnosia who present normal object recognition and minimal or no low-level visual impairments.

5. Conclusions

Here we report an extensive and complete investigation of upright and inverted individual face processing in a case of selective AP. The results indicate an absence of inversion effect in this patient. An overview of the literature supports the view that acquired prosopagnosic patients present an abolished or reduced inversion effect, rather than a rare pattern of inversion superiority that is likely due to low-level visual defects. Our findings reinforce the view that a key aspect of the impairment in AP lies in the inability to form a holistic representation of the individual face.

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REFERENCES

Anaki D, Kaufman Y, Freedman M, and Moscovitch M. Associative (prosop)agnosia without (apparent) perceptual deficits: A case-study. *Neuropsychologia*, 45: 1658–1671, 2007.

Bartlett JC, Searcy JH, and Abdi H. What are the routes to face recognition? In Peterson M and Rhodes G (Eds), *Perception of Faces, Objects and Scenes: Analytic and Holistic Processes*. Oxford: Oxford University Press, 2003: 21–52.

Bartolomeo P, Bachoud-Lévi A-C, De Gelder B, Denes G, Dalla Barba G, Brugières P, et al. Multiple-domain dissociation between impaired visual perception and preserved mental imagery in a patient with bilateral extrastriate lesions. *Neuropsychologia*, 36: 239–249, 1998.

Barton JJS, Keenan JP, and Bass T. Discrimination of spatial relations and features in faces: Effects of inversion and viewing duration. *British Journal of Psychology*, 92: 527–549, 2001.

Barton JJS, Press DZ, Keenan JP, and O'Connor M. Lesions of the fusiform face area impair perception of facial configuration in prosopagnosia. *Neurology*, 58: 71–78, 2002.

Barton JJS, Zhao J, and Keenan JP. Perception of global facial geometry in the inversion effect and prosopagnosia. *Neuropsychologia*, 41: 1703–1711, 2003.

Barton JJS, Cherkasova MV, Press DZ, Intriligator JM, and O'Connor M. Perceptual functions in prosopagnosia. *Perception*, 33: 939–956, 2004.

Behrmann M and Avidan G. Congenital prosopagnosia: Face-blind from birth. *Trends in Cognitive Sciences*, 9: 180–187, 2005.

Behrmann M, Avidan G, Gao F, and Black S. Structural imaging reveals anatomical alterations in inferotemporal cortex in congenital prosopagnosia. *Cerebral Cortex*, 17: 2354–2363, 2007.

Behrmann M, Avidan G, Marotta JJ, and Kimchi R. Detailed exploration of face-related processing in congenital prosopagnosia: 1. behavioral findings. *Journal of Cognitive Neuroscience*, 17: 1130–1149, 2005.

Benton AL. The neuropsychology of facial recognition. *The American Psychologist*, 35: 176–186, 1980.

Benton AL, Sivan AB, Hamsher K, Varney NR, and Spreen O. *Benton Facial Recognition: Stimulus and Multiple Choice Pictures*. Lutz: Psychological Assessment Resources Inc, 1983.

Bodamer J. Die prosopagnosie. *Archiv für Psychiatrie und Nervenkrankheiten*, 179: 6–54, 1947. Partial English translation by Ellis HD and Florence M. *Cognitive Neuropsychology*, 7: 81–105, 1990.

Boutsen L and Humphreys GW. Face context interferes with local part processing in a prosopagnosic patient. *Neuropsychologia*, 40: 2305–2313, 2002.

Bouvier SE and Engel SA. Behavioral deficits and cortical damage loci in cerebral achromatopsia. *Cerebral Cortex*, 16: 183–191, 2006.

Bukach CM, Bud DN, Gauthier I, and Tarr MJ. Perceptual expertise effects are not all or none: Spatially limited perceptual expertise for faces in a case of prosopagnosia. *Journal of Cognitive Neuroscience*, 18: 48–63, 2006.

Busigny T, Robaye L, Dricot L, and Rossion B. Right anterior temporal lobe atrophy and person-based semantic defect: A detailed case study. *Neurocase*, 15(6): 485–508, 2009.

Caldara R, Schyns P, Mayer E, Smith ML, Gosselin F, and Rossion B. Does prosopagnosia take the eyes out from faces? Evidence for a defect in the use of diagnostic facial information in a brain-damaged patient. *Journal of Cognitive Neuroscience*, 17: 1652–1666, 2005.

Crawford JR and Garthwaite PH. Investigation of the single case in neuropsychology: Confidence limits on the abnormality of test scores and test score differences. *Neuropsychologia*, 40: 1196–1208, 2002.

Crawford JR and Howell DC. Comparing an individual's test score against norms derived from small samples. *The Clinical Neuropsychologist*, 12: 482–486, 1998.

Crookes K and McKone E. Early maturity of face recognition: No childhood development of holistic processing, novel face encoding, or face-space. *Cognition*, 111: 219–247, 2009.

Damasio AR, Damasio H, and Van Hoesen GW. Prosopagnosia: Anatomic basis and behavioural mechanisms. *Neurology*, 32: 331–341, 1982.

Davidoff J and Landis T. Recognition of unfamiliar faces in prosopagnosia. *Neuropsychologia*, 28: 1143–1161, 1990.

de Gelder B, Bachoud-Lévi A-C, and Degos J-D. Inversion superiority in visual agnosia may be common to a variety of orientation polarized objects besides faces. *Vision Research*, 38: 2855–2861, 1998.

de Gelder B and Rouw R. Paradoxical configuration effects for faces and objects in prosopagnosia. *Neuropsychologia*, 38: 1271–1279, 2000a.

de Gelder B and Rouw R. Structural encoding precludes recognition of face parts in prosopagnosia. *Cognitive Neuropsychology*, 17: 89–102, 2000b.

de Gelder B and Rouw R. Configural face processing in acquired and developmental prosopagnosia: Evidence for two separate face systems? *NeuroReport*, 11: 3145–3150, 2000c.

Delvenne J-F, Seron X, Coyette F, and Rossion B. Evidence for perceptual deficits in associative visual (prosop)agnosia: A single-case study. *Neuropsychologia*, 42: 597–612, 2004.

Dricot L, Busigny T, and Rossion B. Behavioral and neural evidence for preserved holistic face detection in acquired prosopagnosia [abstract]. *Journal of Vision*, 8: 410a, 2008.

Duchaine BC and Weidenfield A. An evaluation of two commonly used tests of unfamiliar face recognition. *Neuropsychologia*, 41: 713–720, 2003.

Duchaine BC, Yovel G, Butterworth EJ, and Nakayama K. Prosopagnosia as an impairment to face-specific mechanisms: Elimination of the alternative hypotheses in a developmental case. *Cognitive Neuropsychology*, 23: 714–747, 2006.

Farah MJ. *Visual Agnosia: Disorders of Object Recognition and What They Tell us About Normal Vision*. Cambridge, MA: MIT Press, 1990.

Farah MJ, Wilson KD, Drain HM, and Tanaka JR. The inverted face inversion effect in prosopagnosia: Evidence for mandatory, face-specific perceptual mechanisms. *Vision Research*, 35: 2089–2093, 1995a.

Farah MJ, Tanaka JW, and Drain HM. What causes the face inversion effect? *Journal of Experimental Psychology. Human Perception and Performance*, 21: 628–634, 1995b.

Farah MJ, Wilson KD, Drain HM, and Tanaka JR. What is "special" about face perception? *Psychological Review*, 105: 482–498, 1998.

Freire A, Lee K, and Symons LA. The face-inversion effect as a deficit in the encoding of configural information: Direct evidence. *Perception*, 29: 159–170, 2000.

Galli G. Prosopagnosia und normale Gesichtwahrnehmung. *Wiener Zeitschrift für Nervenheilkunde*, 22: 28–37, 1964.

Gauthier I, Behrmann M, and Tarr MJ. Can face recognition really be dissociated from object recognition? *Journal of Cognitive Neuroscience*, 11: 349–370, 1999.

Goffaux V and Rossion B. Face inversion disproportionately impairs the perception of vertical but not horizontal relations between features. *Journal of Experimental Psychology: Human Perception and Performance*, 33: 995–1002, 2007.

Hécaen H and Angelergues R. Agnosia for faces (prosopagnosia). *Archives of Neurology*, 7: 92–100, 1962.

Hochberg J and Galper RR. Recognition of faces: An explanatory study. *Psychological Science*, 9: 619–620, 1967.

Hsiao JH and Cottrell G. Two fixations suffice in face recognition. *Psychological Science*, 19: 998–1006, 2008.

Jacques C and Rossion B. Early electrophysiological responses to multiple face orientations correlate with individual discrimination performance in humans. *NeuroImage*, 36: 863–876, 2007.

Jacques C, d'Arripe O, and Rossion B. The time course of the face inversion effect during individual face discrimination. *Journal of Vision*, 7: 1–9, 2007.

Joubert S, Felician O, Barbeau E, Sontheimer A, Barton JJ, Ceccaldi M, et al. Impaired configurational processing in a case of progressive prosopagnosia associated with predominant right temporal lobe atrophy. *Brain*, 126: 2537–2550, 2003.

Joubert S, Rossion B, and Busigny T. L'évaluation neuropsychologique de la prosopagnosie. In Barbeau E, Joubert S, and Felician O (Eds), *Traitement et reconnaissance des visages: Du percept à la personne*. Marseille: Solal, 2008: 41–78.

Leder H and Carbon CC. Face-specific configural processing of relational information. *British Journal of Psychology*, 97: 19–29, 2006.

Levin LA. Topical diagnosis of chiasmal and retrochiasmal disorders. In Miller NR and Newman NJ (Eds), *Walsh & Hoyt's Clinical Neuro-Ophthalmology*. Baltimore: Williams and Wilkins, 1999: 503–574.

Levine DN and Calvanio R. Prosopagnosia: A defect in visual configural processing. *Brain and Cognition*, 10: 149–170, 1989.

Marotta JJ, McKeeff TJ, and Behrmann M. The effects of rotation and inversion on face processing in prosopagnosia. *Cognitive Neuropsychology*, 19: 31–47, 2002.

Mazard A, Schiltz C, and Rossion B. Recovery from adaptation to facial identity is larger for upright than inverted faces in the human occipito-temporal cortex. *Neuropsychologia*, 44: 912–922, 2006.

McKelvie SJ. Emotional expression in upside-down faces: Evidence for configurational and componential processing. *The British Journal of Social Psychology*, 34: 325–334, 1995.

McNeil JE and Warrington EK. Prosopagnosia: A reclassification. *The Quarterly Journal of Experimental Psychology A*, 43: 267–287, 1991.

Meadows JC. The anatomical basis of prosopagnosia. *Journal of Neurology, Neurosurgery and Psychiatry*, 37: 489–501, 1974.

Mondloch CJ, Le Grand R, and Maurer D. Configural face processing develops more slowly than featural face processing. *Perception*, 31: 553–566, 2002.

Morgan CL. *An Introduction to Comparative Psychology*. London: Walter Scott, 1894.

Murray JE. The ups and downs of face perception: Evidence for holistic encoding of upright and inverted faces. *Perception*, 33: 387–398, 2004.

Nilsson D, Malmgren K, Rydenhag B, and Frisen L. Visual field defects after temporal lobectomy – comparing methods and analysing resection size. *Acta Neurologica Scandinavica*, 110: 301–307, 2004.

Nunn JA, Postma P, and Pearson R. Developmental prosopagnosia: Should it be taken at face value? *Neurocase*, 7: 15–27, 2001.

Orban de Xivry JJ, Ramon M, Lefèvre P, and Rossion B. Reduced fixation of the eyes area of personally familiar faces following acquired prosopagnosia. *Journal of Neuropsychology*, 2: 245–258, 2008.

Purcell DG and Stewart AL. The face-detection effect: Configuration enhances detection. *Perception and Psychophysics*, 43: 355–366, 1988.

Quaglino A and Borelli G. Emiplegia sinistra con amaurosi – guarigione – perdita totale della percezione dei colori e della memoria della configurazione degli oggetti. *Giornale d'Oftalmologiia Italiano*, 10: 106–117, 1867.

Rakover SS and Teucher B. Facial inversion effects: Parts and whole relationship. *Perception and Psychophysics*, 59: 752–761, 1997.

Ramon M and Rossion B. 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, 2010.

Riddoch MJ and Humphreys GW. A case of integrative visual agnosia. *Brain*, 110: 1431–1462, 1987.

Riddoch MJ, Johnston RA, Bracewell RM, Boutsen L, and Humphreys GW. Are faces special? A case of pure prosopagnosia. *Cognitive Neuropsychology*, 25: 3–26, 2008.

Righart R and de Gelder B. Impaired face and body perception in developmental prosopagnosia. *Proceedings of the National Academy of Sciences of the United States of America*, 104: 17234–17238, 2007.

Robbins R and McKone E. No face-like processing for objects-of-expertise in three behavioural tasks. *Cognition*, 103: 34–79, 2007.

Rondot P and Tzavaras A. La prosopagnosie après vingt années d'études cliniques et neuropsychologiques. *Journal de Psychologie Normale et Pathologique*, 66: 133–165, 1969.

Russell R, Biederman I, Nederhouser M, and Sinha P. The utility of surface reflectance for the recognition of upright and inverted faces. *Vision Research*, 47: 157–165, 2007.

Rossion B. Picture-plane inversion leads to qualitative changes of face perception. *Acta Psychologica*, 128: 274–289, 2008.

Rossion B and Boremanse A. Nonlinear relationship between holistic processing of individual faces and picture-plane rotation: Evidence from the face composite illusion. *Journal of Vision*, 8: 1–13, 2008.

Rossion B, Caldara R, Seghier M, Schuller A-M, Lazeyras F, and Mayer E. A network of occipito-temporal face-sensitive areas besides the right middle fusiform gyrus is necessary for normal face processing. *Brain*, 126: 2381–2395, 2003.

Rouw R and de Gelder B. Impaired face recognition does not preclude intact whole face perception. *Visual Cognition*, 9: 689–718, 2002.

Santos IM and Young AW. Effects of inversion and negation on social inferences from faces. *Perception*, 37: 1061–1078, 2008.

Saumier D, Arguin M, and Lassonde M. Prosopagnosia: A case study involving problems in processing configural information. *Brain and Cognition*, 46: 255–316, 2001.

Scapinello KF and Yarmey AD. The role of familiarity and orientation in immediate and delayed recognition of pictorial stimuli. *Psychonomic Science*, 21: 329–331, 1970.

Schiltz C, Sorger B, Caldara R, Ahmed F, Mayer E, Goebel R, et al. Impaired face discrimination in acquired prosopagnosia is associated with abnormal response to individual faces in the right middle fusiform gyrus. *Cerebral Cortex*, 16: 574–586, 2006.

Schneider W, Eschman A, and Zuccolotto A. *E-Prime Reference Guide*. Pittsburgh: Psychology Software Tools Inc., 2002.

Schweich M and Bruyer R. Heterogeneity in the cognitive manifestations of prosopagnosia: The study of a group of single cases. *Cognitive Neuropsychology*, 10: 529–547, 1993.

Sekunova A and Barton JJ. 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: 1129–1135, 2008.

Sergent J. An investigation into component and configural processes underlying face perception. *British Journal of Psychology*, 75: 221–242, 1984.

Sergent J and Signoret J-L. Varieties of functional deficits in prosopagnosia. *Cerebral Cortex*, 2: 375–388, 1992.

Sergent J and Villemure JG. Prosopagnosia in a right hemispherectomized patient. *Brain*, 112: 975–995, 1989.

Sorger B, Goebel R, Schiltz C, and Rossion B. Understanding the functional neuroanatomy of prosopagnosia. *NeuroImage*, 35: 836–852, 2007.

Tanaka JW and Farah MJ. Parts and wholes in face recognition. *Quarterly Journal of Experimental Psychology*, 46A: 225–245, 1993.

Tanaka JW and Sengco JA. Features and their configuration in face recognition. *Memory and Cognition*, 25: 583–592, 1997.

Thomas C, Avidan G, Humphreys K, Jung KJ, Gao F, and Behrmann M. Reduced structural connectivity in ventral visual cortex in congenital prosopagnosia. *Nature Neuroscience*, 12: 29–31, 2009.

Townsend JT and Ashby FG. *Stochastic Modelling of Elementary Psychological Processes*. London: Cambridge University Press, 1983.

Valentine T and Bruce V. The effect of race, inversion and encoding activity upon face recognition. *Acta Psychologica*, 61: 259–273, 1986.

Warrington EK. *Recognition Memory Test*. Windsor, Berkshire: NFER, 1984.

Yin RK. Looking at upside-down faces. *Journal of Experimental Psychology*, 81: 141–145, 1969.

Yogarajah M, Focke NK, Bonelli S, Cercignani M, Acheson J, Parker GJ, et al. Defining Meyer's loop-temporal lobe resections, visual field deficits and diffusion tensor tractography. *Brain*, 132: 1656–1668, 2009.

Young AM, Hellawell D, and Hay DC. Configural information in face perception. *Perception*, 10: 747–759, 1987.

Yovel G and Kanwisher N. The neural basis of the behavioral face-inversion effect. *Current Biology*, 15: 2256–2262, 2005.