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Face-specific impairment in holistic perception following focal lesion of the right anterior temporal lobe

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ABSTRACT

Recent studies have provided solid evidence for pure cases of prosopagnosia following brain damage. The patients reported so far have posterior lesions encompassing either or both the right inferior occipital cortex and fusiform gyrus, and exhibit a critical impairment in generating a sufficiently detailed holistic percept to individualize faces. Here, we extended these observations to include the prosopagnosic patient LR (Bukach, Bub, Gauthier, & Tarr, 2006), whose damage is restricted to the anterior region of the right temporal lobe. First, we report that LR is able to discriminate parametrically defined individual exemplars of nonface object categories as accurately and quickly as typical observers, which suggests that the visual similarity account of prosopagnosia does not explain his impairments. Then, we show that LR does not present with the typical face inversion effect, whole-part advantage, or composite face effect and, therefore, has impaired holistic perception of individual faces. Moreover, the patient is more impaired at matching faces when the facial part he fixates is masked than when it is selectively revealed by means of gaze contingency. Altogether these observations support the view that the nature of the critical face impairment does not differ qualitatively across patients with acquired prosopagnosia, regardless of the localization of brain damage: all these patients appear to be impaired to some extent at what constitutes the heart of our visual expertise with faces, namely holistic perception at a sufficiently fine-grained level of resolution to discriminate exemplars of the face class efficiently. This conclusion raises issues regarding the existing criteria for diagnosis/classification of patients as cases of apperceptive or associative prosopagnosia.

1. Introduction

1.1. Apperceptive and associative prosopagnosia

For most of us, recognizing a friend by his/her face is so easy and natural that we are usually unaware of the complexity of the operations at play during face recognition, a function that has been the topic of many investigations in experimental (neuro)psychology over the past decades (Calder, Rhodes, Johnson, & Haxby, 2011; Bruce & Young, 2012). Traditionally, experimental psychologists and cognitive neuropsychologists have divided the process of face recognition into several sub-functions or sub-processes (Bruce & Young, 1986). These processes are thought to be carried out by distinct brain structures, organized in a network (e.g., Sergent, Otha, & MacDonald, 1992; Allison, Puce, Spencer, & McCarthy, 1999; Haxby, Hoffman, & Gobbini, 2000; Gobbini & Haxby, 2007; Fox, Iaria, & Barton, 2009; Weiner & Grill-Spector, 2010; Rossion, Hanseeuw, & Dricot, 2012; Pyles, Verstynen, Schneider, & Tarr, 2013).

A major distinction in the field is made between the perceptual and mnesic aspects of face recognition. For instance, several authors have applied the apperceptive/associative classification of visual agnosia, called “psychic blindness” by Lissauer (1890), to the domain of faces (De Renzi, 1986; De Renzi, Faglioni, Grossi, & Nichelli, 1991; Sergent & Signoret, 1992a, 1992b; Barton, 2003). These authors argued that there are at least two separate forms of the inability to recognize faces following brain damage: an apperceptive and an associative form of prosopagnosia. Patients with apperceptive prosopagnosia are unable to perceive faces properly, while patients with associative prosopagnosia are unable to associate a correct percept of a face with stored memories about this face. Apperceptive prosopagnosia has been linked to posterior occipito-temporal lesions, whereas associative prosopagnosia has

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been associated with lesions of the anterior part of the temporal lobe, in particular in the right hemisphere (Gross & Sergent, 1992; Sergent & Signoret, 1992b; Barton, Cherkasova, & Hefter, 2004; Pancaroglu et al. 2011).

The vast majority of impairments in face recognition following damage to the anterior temporal lobe has been reported in the context of neurodegenerative diseases, such as the right temporal variant of frontotemporal dementia (Tyrrell, Warrington, Frackowiak, & Rossor, 1990; Barbarotto, Capitani, Spinnler, & Trivelli, 1995; Evans, Heggs, Antoun, & Hodges, 1995; Gentileschi, Sperber, & Spinnler, 1999, 2001; Gainotti, Barbier, & Marra, 2003; Gainotti, Ferraccioli, Quaranta, & Marra, 2008; Gorno-Tempini et al., 2004; Thompson et al., 2004; Joubert et al., 2006; Busigny, Robaye, Dricot, & Rossion, 2009). However, these patients are usually also impaired in recognizing individuals by their names and voices. Since face recognition impairment is only one symptom of (somewhat diffuse) damage in the anterior temporal lobe, it might be more appropriate to characterize these patients as having "multimodal person recognition disorder" rather than "associative prosopagnosia" (Gainotti, 2013).

More rarely, sudden focal brain damage to the anterior temporal lobe due to herpes simplex encephalitis (Warrington & McCarthy, 1988; Hanley, Young, & Pearson, 1989; Sergent & Poncet, 1990; Haslam, Cook, & Coltheart, 2001; Barton, Hanif, & Ashraf, 2009; Dalrymple et al., 2011; Pancaroglu et al., 2011), closed head injury (Kapur, Ellison, Smith, McLellan, & Burrows, 1992; Barton, Zhao, & Keenan, 2003), or following anterior temporal lobe resection in the context of epileptic seizures resistant to medication (Ellis, Young, & Critchley, 1989; Tippett, Miller, & Farah, 2000; Glosser, Salvucci, & Chiaravalloti, 2003; Chiaravalloti & Glosser, 2004; Drane et al., 2008; Pancaroglu, Johnston, Sekunova, Duchaine, & Barton, 2012) (see Table 1) can all result in impairments in face recognition. However, the majority of these patients are also impaired at recognizing individuals by their names and voices.

1.2. Perceptual impairment in associative prosopagnosia

The studies listed above suggest that patients with right anterior temporal lobe damage are impaired at memorizing new faces, identifying familiar faces and retrieving semantic information about familiar faces. In general, these patients have been reported as being unimpaired in face *perception*, i.e., the ability to build a proper visual representation – an internal image – of a face. For instance, most patients were able to match simultaneously presented pictures of unfamiliar faces, as in the Benton Face Recognition Test (BFRT, Benton & van Allen, 1968) or similar tests (Warrington & McCarthy, 1988; Ellis et al., 1989; Hanley et al., 1989; Sergent & Poncet, 1990; Kapur et al., 1992; Tippet et al., 2000; Haslam et al., 2001; Glosser et al., 2003; Chiaravalloti & Glosser, 2004; Barton et al., 2009; Dalrymple et al., 2011; see Table 1). However, importantly, with the exception of a single-patient study (Sergent & Poncet, 1990), response times were never reported. Consequently, whether these patients relied on a slow feature-by-feature strategy to match faces, as reported in many cases of prosopagnosia with face perception impairment (e.g. Newcombe, 1979; McNeil & Warrington, 1991; Young, Flude, Hay, & Ellis, 1993; Mattson, Levin, & Grafman, 2000; Rossion et al., 2003; Delvenne, Seron, Coyette, & Rossion, 2004), remains unknown. Moreover, there are good reasons to doubt that perception of faces is intact in these patients. In a review of 99 cases of associative visual agnosia, Farah (1990/2004) reported that most patients characterized as being of the 'associative' form were abnormally sensitive to the visual quality of the stimuli, and performed poorly when recognizing line drawing stimuli or stimuli presented tachistoscopically. Most of these patients' recognition errors were visual in nature. When patients did copy drawings reasonably well, they were described as using a "slavish, line-by-line, and piecemeal" strategy (Farah, 1990/2004, p. 74). Although these observations concern object rather than face recognition, they raise issues around the diagnosis criteria of a purely associative form of prosopagnosia.

1.3. Nature of the perceptual impairment in apperceptive prosopagnosia

There is now converging evidence supporting the view that patients with acquired apperceptive prosopagnosia present with impaired configural/holistic face perception (for a review see Busigny, Joubert, Felician, Ceccaldi, & Rossion, 2010a). While their perception of face parts is relatively well preserved, these patients seem unable to integrate these different parts into a single, unified

Table 1
Face perception results of patients reported with anterior temporal lesions and presenting with face recognition difficulties.

Patient	Etiology	Face perception	Results
RFR (Warrington & McCarthy, 1988)	HSE	OK	18/20 (same/diff matching task)
BD (Hanley et al., 1989)	HSE	OK	46/54 (BFRT)
PV (Sergent & Poncet, 1990)	HSE	OK	46/54, 6min21 (BFRT)
TG (Haslam et al., 2001)	HSE	OK	43/54 (BFRT)
B-AT1 (Barton et al., 2009; Dalrymple et al., 2011)	HSE	OK	45/54 (BFRT) 100% (same/diff discrimination, FAB) 48% of errors (CFPT, mean = 36.7; SD = 12.2)
R-AT2 (Barton et al., 2009)	HSE	OK	47/54 (BFRT) 90% (same/diff discrimination, FAB) 40% of errors (CFPT, mean = 36.7; SD = 12.2)
LT (Kapur et al., 1992)	CHI	OK	Preserved (BFRT)
TS/008 (Barton et al., 2003; Barton, 2008)	CHI	impaired	24/54 (BFRT) No face geometry effect
KS (Ellis et al., 1989)	RATL	OK	45/54 (BFRT)
CT (Tippett et al., 2000)	RATL	OK	43/54 (BFRT) 91% (1581 ms) upright faces 78% (1641 ms) inverted faces Normal performance + normal FIE
R-AT1 (Barton et al., 2009)	RATL	OK	41/54 (BFRT) 58% of errors (CFPT, mean = 36.7; SD = 12.2)
26 patients (Glosser et al., 2003)	RATL	OK	$Z = -0.71$ (0,22) (BFRT) compared to controls
38 patients (Chiaravalloti & Glosser, 2004)	RATL	OK	± 44/54 (before surgery) (BFRT) ± 43/54 (after surgery) (BFRT)

HSE = Herpes Simplex Encephalitis.
CHI = Closed Head Injury.
ATL = Right Anterior Temporal Lobectomy.
BFRT = Benton Face Recognition Test (Benton & Van Allen, 1968).
FAB = Florida Affect Battery (Bowers et al., 1991).
CFPT = California Face Perception Test (Duchaine et al., 2007).

representation (Davidoff, Matthews, & Newcombe, 1986; Levine & Calvanio, 1989; Sergent & Villemure, 1989; Spillmann, Laskowski, Lange, Kasper, & Schmidt, 2000; Saumier, Arguin, & Lassonde, 2001; Boutsen & Humphreys, 2002; Barton, Press, Keenan, & O'Connor, 2002; Barton, 2008; Riddoch, Johnston, Bracewell, Boutsen, & Humphreys, 2008; Wilkinson et al., 2009; Busigny et al., 2010a; Ramon, Busigny, & Rossion, 2010).

A wide variety of methodological paradigms have been used to test holistic/configural face perception in prosopagnosia. In most studies, the patients tested were also impaired at object recognition (e.g., Boutsen & Humphreys, 2002; Levine & Calvanio, 1989). More recently, classical paradigms developed for testing holistic/configural face perception in the normal population have been used to assess patients with intact object recognition ('pure prosopagnosia'). More specifically, impairment in holistic perception was evidenced in prosopagnosia by the absence or reduction of the face inversion effect (Busigny & Rossion, 2010a; Busigny et al., 2010a), a lack of advantage in processing parts embedded in whole faces as compared to isolated parts (Busigny et al., 2010a; Ramon et al., 2010) and an abnormal composite face effect (Busigny et al., 2010a; Ramon et al., 2010). A novel approach to understand difficulties in holistic perception of individual faces has also been developed using gaze-contingency (Van Belle, de Graef, Verfaillie, Busigny, & Rossion, 2010a; Van Belle et al., 2011), a method traditionally used to investigate the perceptual span in reading by selectively revealing/masking a portion of the visual field (Rayner, 1998). Introducing this approach in face perception research, Van Belle et al. (2010a, 2011) showed that the performance pattern of patients with acquired prosopagnosia in a face matching task was reversed in comparison to normal observers. That is, compared to their performance with faces presented in full view, the patients showed almost no decrease in performance when only one facial part (eye, mouth, nose, etc.) was available at a time (forcing part-based analysis). In contrast, when the fixated part was selectively masked (promoting holistic perception) patients showed an increased impairment.

Altogether, these observations support a generalized account of acquired prosopagnosia in which the critical impairment concerns *holistic perception of an individual face*. Among all visual categories, faces would be the only one for which fine-grained differentiation (i.e., individualization) would *require* holistic perception. This would lead to the observation of rare cases of pure prosopagnosia following brain damage (Busigny et al., 2010a).

So far, this latter approach, as well as the other detailed investigations testing the holistic face perception hypothesis, have only been applied to cases of prosopagnosia presenting with clear perceptual impairments with faces, following posterior (occipital inferior and fusiform) brain damage. In the present study, we tested a case of acquired prosopagnosia with damage restricted to the right anterior temporal lobe, in order to test the hypothesis that even in such cases there is impairment in holistic perception of individual faces.

This hypothesis was prompted by two further observations. First, Barton and colleagues have shown that the patient TS/008, with bilateral anterior temporal lobe lesions (sparing the lingual and fusiform gyri bilaterally), showed some difficulties in face perception in addition to his strong impairment in face memory, face familiarity and famous face recognition (Barton et al., 2003; Barton, 2008). More precisely, TS was severely impaired at the Benton Face Recognition Test (25/54) and showed reduced sensitivity to the global relations between facial parts with simultaneously presented faces (Barton et al., 2003). Second, patient LR (Bukach, Bub, Gauthier, & Tarr, 2006), presenting with right anterior temporal damage and memory deficits for faces, also seemed to be impaired at face perception. Although LR performed within the normal range at the Benton Face Recognition Test (49/54), he was described as being particularly slow, as evidenced by a dramatically low score of 12/54 when a 17 s cutoff was administered for each trial (Bukach et al., 2006). In addition, the patient was impaired at extracting diagnostic information at the level of the eyes, a characteristic shared by several cases of acquired prosopagnosia with an impairment of perceptual nature (Caldara et al., 2005; Busigny et al., 2010a). Bukach et al. (2006) concluded their case study by stating that LR had preserved holistic processing of faces, because his matching of two top halves of faces (same or different) was influenced by the congruency (same or different) of the bottom halves. However, this conclusion needs to be qualified because it was based on a single test, and with only two control participants. Moreover, the congruency paradigm used to infer normality of holistic face processing lacked a control condition (misaligned face halves) and presented other significant methodological limitations (Rossion, 2013).

Here, we aimed to study holistic face perception more extensively in the same patient LR. First, we made a novel assessment of LR's recognition impairment and its specificity to faces vs. other familiar object categories. Specifically, we asked the patient to discriminate exemplars of both face and nonface objects at a fine-grained level, using a series of tasks developed recently in the context of apperceptive prosopagnosia (Busigny, Graf, Mayer, & Rossion, 2010b). Next, we assessed LR's holistic face perception using the following tests: face inversion, whole-part advantage and composite face paradigms, and gaze-contingency during face matching.

2. Methods

2.1. LR's case description

LR is a male born in 1953 who received a head wound in a motor vehicle accident at 19 years of age. As described in Bukach et al. (2006, 2008), LR was thrown from the front passenger seat of a truck onto the gearshift. The gear lever was missing the usual plastic cap covering the top, and LR received a penetrating head wound when the hollow metal tube of the uncapped gearshift impaled his lower left cheek in front of the jaw, passing through the left intracranial cavity and sphenoid sinus. The shaft then entered the right cavernous sinus, clipping the right internal carotid artery and injuring the abducens nerve and the ophthalmic and maxillary divisions of the trigeminal nerve. It pierced the right temporal lobe, leaving a bone fragment in the superficial aspect of the middle temporal gyrus. LR subsequently developed a right temporal intracerebral hematoma, which was relieved through a surgeryrequiring clipping of the right internal carotid artery (Fig. 1A). CT scans revealed ablation of the anterior and inferior sections of the right temporal lobe affecting the amygdala, but sparing posterior regions including the fusiform gyrus (Fig. 1B–D). As a result of the clip, LR is not able to undergo magnetic resonance imaging (MRI). Visual acuity a year following the accident was 20/20 in both eyes with corrective lenses, and visual fields were full. However, following the accident, LR was no longer able to recognize faces, including highly familiar individuals like his own daughter. To recognize people, he claims to rely primarily on distinctive features and context.

LR performed above average on all tests of memory, object naming, reading and perception, excluding a general cognitive disorder as a cause of his face recognition problems (see Bukach et al., 2006). His only abnormalities were on tests involving faces. As mentioned above, LR showed an extremely slow and feature-based strategy when carrying out the Benton Face Recognition Test (49/54 but 55.18 s per trial). Regarding face memory, LR obtained an impaired score of 38/50 (5th percentile) in the Warrington Recognition Memory Test (Warrington, 1984). When presented with 121 photos of famous persons, he was able to provide correct names for only 23 famous faces. In another task requiring identifying 35 famous people from their face or their name, LR was able to correctly identify all of them by their names by providing correct semantic information, but in contrast, he was only able to identify 15 people from their faces (Bukach et al., 2008).

A new assessment of face processing abilities, conducted in 2010 by the authors of the present paper, confirmed LR's face recognition impairment. In a first task, LR recognized 13 out of 40 famous faces (of individuals from the US and UK, including actors, singers and politicians). When provided with their names, he knew 33 out of 40 of these faces. Excluding the 7 individuals unknown by name, his face recognition score remains very low (13/33, or 39.4%). LR's score was significantly lower ($Chi2_1 = 38.34$, $p < 0.001$) than his partner's (55 years old), who recognized 31 faces out of 40 (his partner knew 34 of them when provided with their names).

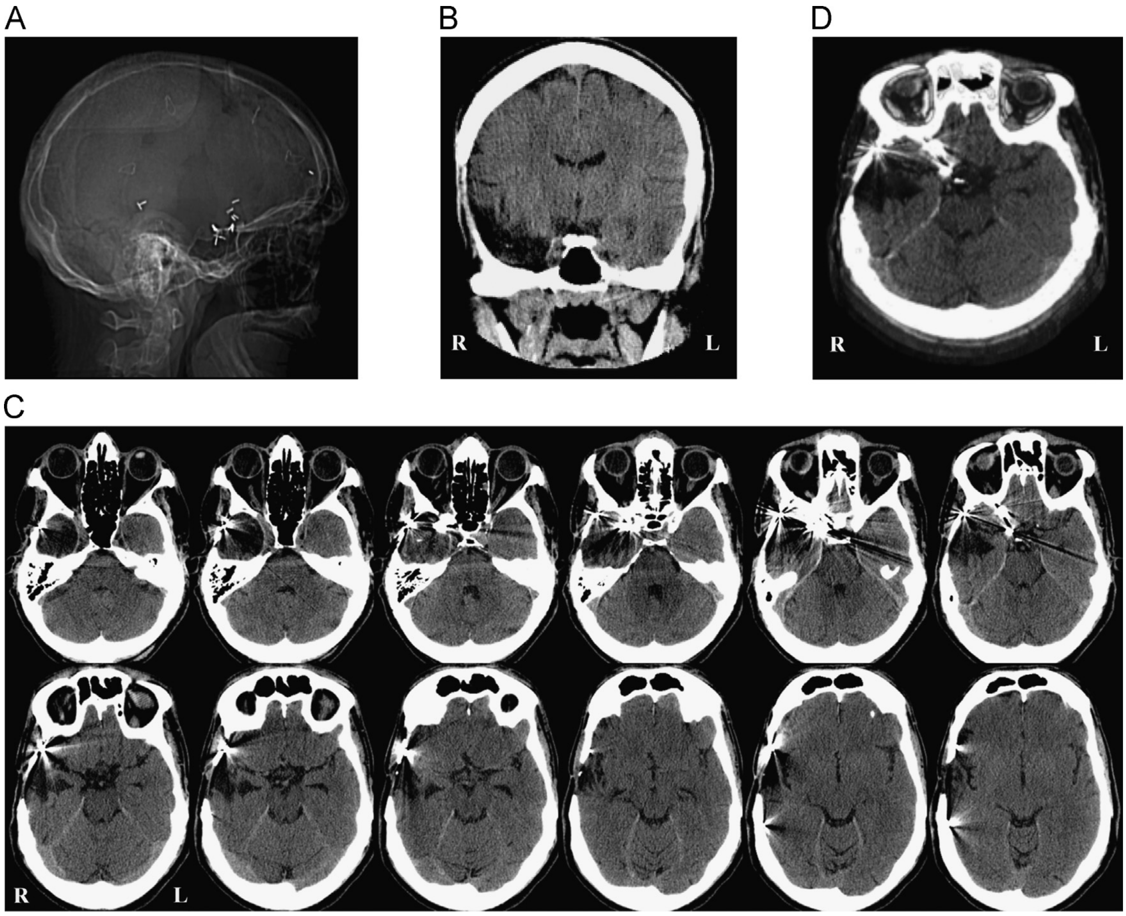

Fig. 1. LR's lesions located in the anterior portion of the right temporal lobe. (A) Clips, (B) Coronal view (from Bukach et al., 2006), (C) Multiple 2D transversal views and (D) 3D view created from 7 transversal views.

In the next tasks, LR's face memory impairment was confirmed by the Cambridge Face Memory Test of Duchaine and Nakayama (2006; LR'score: 42/72; $Z=-2.01$) and on an old/new face recognition task (Busigny et al., 2010b, task 3), in which he obtained a score of 30/50 (not different from chance; $Chi^2=2$, $p=0.16$). Altogether, these results clearly illustrate LR's massive impairment in face recognition.

2.2. General methodological considerations

LR was administered a set of seven behavioral tasks, including one experiment with gaze-contingency. These experiments were conducted during three time periods, in February 2008, May 2009, and June 2010. Ten healthy male control participants were also tested in each experiment (7 in the last experiment with gaze contingency), matched to LR for socio-economic background and age. Some of the control data were collected in previous studies (Busigny, Joubert et al., 2010; Busigny, Graf et al., 2010), and these data were included in the present study to have ten controls for each experiment. Control participants had no history of neurological or vascular disease, head injury or alcohol abuse, and did not have cognitive complaints. All participants gave informed consent.

In the first six behavioral experiments, the stimuli were presented using E-Prime 1.1 (Schneider, Eschman, & Zuccolotto, 2002). The patient was positioned at about 40 cm from the screen. He was asked to provide a binary response using the keyboard of the laptop computer. In the seventh experiment, concerning gaze-contingency, eye movements were recorded using an SR Eyelink 1000 monocular desktop mount, tracking the dominant (the non-dominant eye was covered). Stimuli were displayed on a 21″ CRT Viewsonic Graphic series G225f monitor with a spatial resolution of 1024×768 pixels, and a temporal resolution of 75 Hz at a distance of 62 cm.

Percentages of correct responses and response times (RTs) on correct trials were calculated. Outlier response times were discarded when they were more than two standard deviation of the average response time of each participant in the condition considered.

Statistical analyses were conducted with SPSS 18.0 within the framework of one-tailed hypothesis (0.05 p-value), except when mentioned otherwise in the text. For intra-subject statistical analyses (conducted on patient LR), Chi-square tests were conducted on accuracy scores and independent sample T-tests were performed on response times. For across subject statistical analyses (conducted on the normal controls considered as a group), paired sample t-tests were used on accuracy rates and response times. To compare the results of LR to the control participants, the modified t-test of Crawford and Howell (1998) for single-case studies was used with a 0.05 p-value within the framework of a unilateral hypothesis, because we expected worse performance for the patient than the controls. Consequently, for all scores associated with a p-value under 0.05, LR was considered as being out of normal range. Analyses were conducted with a computerized version of the Crawford & Howell's method: *SINGLIMS.EXE: Point estimate and confidence limits on the abnormality of a test score* (Crawford & Garthwaite, 2002). Experiments 6 and 7 only required comparison of multiple variables. Thus, for both intra-subject and across subject analyses we used ANOVAs. we used ANOVAs. Furthermore, for intra-subject analyses we used a non-parametrical bootstrapping procedure on accuracy rates. The bootstrap procedure was done with 1000 iterations, in which N random numbers (N=the number of trials) were generated from a binomial distribution, with a probability distribution equal to the accuracy in the condition under consideration. For each iteration, the accuracy rate was calculated and sorted: the 95% confidence interval corresponds to the 25th and 975th generated accuracy rate.

3. Experiments

3.1. Is LR's Visual recognition impairment limited to faces?

3.1.1. Experiment 1. face and object discrimination at the individual level

3.1.1.1. Material and procedure. The patient and control participants were shown individual pictures from different object categories: birds, boats, cars, chairs and faces (the task was originally described in Schiltz et al., 2006 and later in Busigny et al., 2010b). In a delayed two-alternative forced choice decision task, participants were first presented with a target stimulus belonging to one of the five categories for one second. Following

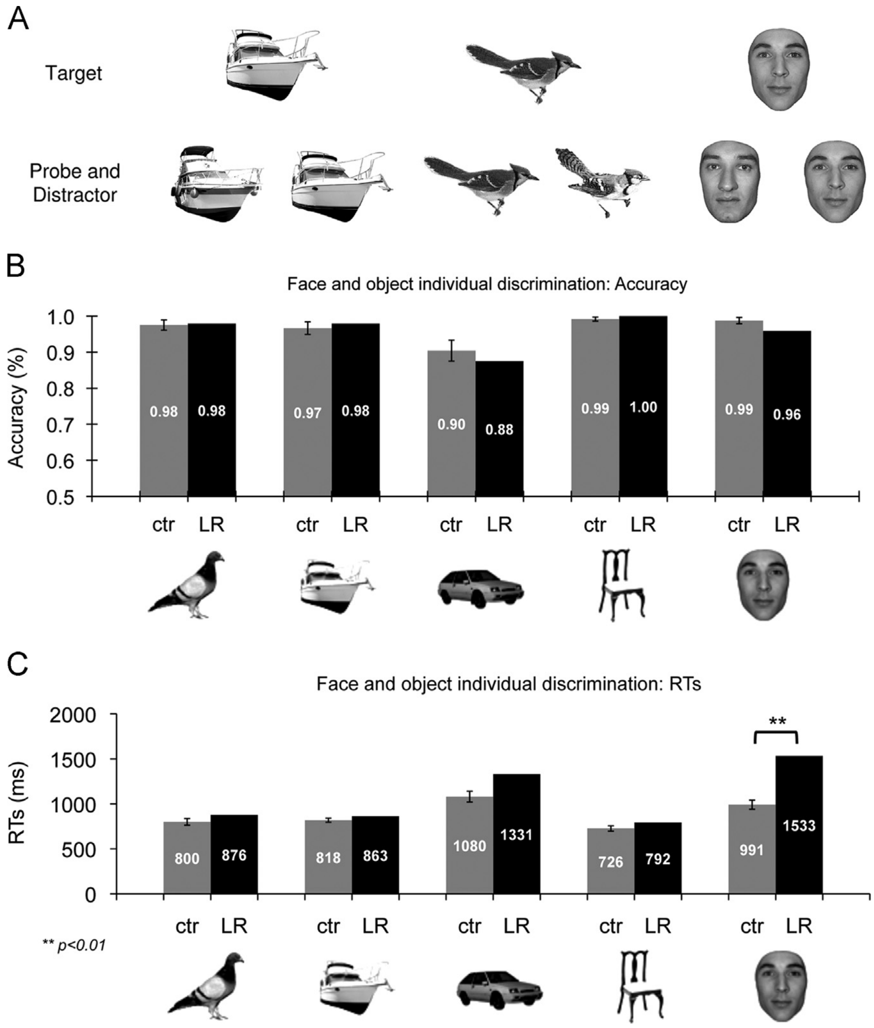

Fig. 2. Experiment 1: Face and object discrimination at the individual level. (A) Examples of targets, probes and distractors in the intra-category discrimination. (B) Accuracy rates for LR and controls in intra-category discrimination. (C) Response times on correct trials for LR and controls in intra-category discrimination. Error bars for controls indicate standard errors. Asterisks refer to the significance of the *t*-value provided by the modified *t*-test of Crawford and Howell (1998), performed between LR and controls.

a brief delay (1000 ms), they have to discriminate the target from a distractor. The distractor belongs to the same (intra-category discrimination, half of the trials, Fig. 2A) or to another visual category (inter-category discrimination). To encode the response, participants are asked to press a key corresponding to the position of the stimulus (i.e., right-key if right-stimulus; left-key if left-stimulus); no time constraints were applied but the participants were instructed to respond as accurately and as quickly as possible. Photographs of faces were cropped (i.e., external cues were removed) and for all objects any "external" cue was also removed (e.g., license plates of cars). Twenty-four grayscale pictures of each category were used in the two conditions (inter- and intra-category). The experiment was divided into four blocks of sixty randomized trials. The stimuli subtended approximately the following sizes, respectively in height and width: birds ($6.4^\circ \times 9.9^\circ$), boats ($8.5^\circ \times 9.9^\circ$), cars ($5^\circ \times 9.9^\circ$), chairs ($9.9^\circ \times 5.7^\circ$) and faces ($9.2^\circ \times 7.1^\circ$). The pictures were displayed on a white background.

3.1.1.2. Control participants. Ten healthy controls were tested (mean age: 57; SD: 7.12).

3.1.1.3. Results and discussion. For the between-category discrimination (distractor from another category), performance was at ceiling for all participants and categories (global performance of LR: 100%; average global performance of controls: 99.6%, SD: 0.29; $t_9 = 1.315$, $p = 0.11$). In the within-category discrimination (distractor from the same category), LR performed in the normal range for the five categories, including faces (all *p*-values above 0.18) (Fig. 2B). Regarding RTs, LR performed in the normal range for the four non-face categories (all *p*-values above 0.12). However, he was significantly slowed down for faces (LR: 1533 ms; controls' mean: 991 ms, SD: 158; $t_9 = 3.271$, $p < 0.01$), even though faces were not the most difficult items to discriminate for normal controls (Fig. 2C). These results show that the patient probably uses an abnormal strategy to process faces. His impairment does not seem to extend to other visual categories.

3.1.2. Experiment 2. discrimination of similar items: cars and faces

3.1.2.1. Material and procedure. This task was aimed at assessing LR's ability to discriminate pictures of cars and faces presented at different levels of physical similarity (a task described in Busigny, Joubert et al., 2010; Busigny, Graf et al., 2010). Twenty photographs of cars were selected and were morphed two-by-two with Morph™. We extracted 5 distractors in increasing order of dissimilarity from each original car photograph (20, 40, 60, 80 and 100%). For faces, 32 color laser scanned pictures of faces (from the Max-Planck Institute, Germany) were used (half female) and were morphed two-by-two (Morphable Model For The Synthesis

Of 3D Faces; Blanz & Vetter, 1999). As for pictures of cars, we used 5 levels of (dis)similarity for the distractors (20, 40, 60, 80 and 100%). Overall, we used 32 trials for each level. The car stimuli subtended approximately $5.7^\circ \times 12.7^\circ$ and the face stimuli $7.8^\circ \times 6.4^\circ$, at 40 cm from the monitor. They were displayed on a white background. The participants had to perform a 2-alternative forced-choice (2AFC) matching task. The target was presented first during 2000 ms, followed by an ISI (1000 ms) and then a screen appeared showing the target together with a distractor. This distractor consisted in one of five levels of morphing of the target item. The patient had to decide which of the two probe pictures was the same as the previous one by pressing a corresponding key. The experiment was divided into four blocks of 80 trials (blocks 1 & 3 displayed faces and blocks 2 & 4 displayed cars, and the order was kept identical for every control and the patient).

Typical participants are expected to perform better and faster with the most dissimilar distractor, with a progressive increase of error rates and RTs as the visual similarity between the target and distractor increases. If LR's face processing impairment is due to an increased difficulty with visually similar items, then the slope of increase of error rates and correct RTs should be steeper for LR than for normal controls.

3.1.2.2. Control participants. Ten healthy controls were tested (mean age: 59.9; SD: 6.96).

3.1.2.3. Results and discussion

3.1.2.3.1. Car pictures. Overall, LR performed in the normal range in accuracy and correct RTs (see Table 2). In accuracy, LR was in the normal range for the 5 levels (all p-values above 0.21; see Table 2 and Fig. 3B). For the most difficult level, in which the dissimilarity between the target and the distractor is only of 20%, LR scored at chance level, as did four of the controls. We also compared the regression slopes of LR and controls (see Armitage, 1980): LR's slope did not differ significantly from controls ($t_6=0.284$, $p=0.79$).

For correct RTs, LR was also in the normal range for the 5 levels (all p-values above 0.08; see Table 2 and Fig. 3B) and his slope did not differ from that of the controls ($t_6=0.724$, $p=0.49$).

As expected, control participants showed decreased of accuracy and increased response time with the degree of dissimilarity: the more similar the distractor was to the target (from 100% difference to 20% difference), the less efficient were the controls. The decrease in performance with decreasing levels of dissimilarity was also noticeable for accuracy and RTs for LR. He obtained exactly the same results as controls: at each level, his accuracy and correct response times were in the normal range, his pattern of performance following exactly the same slope as the controls.

3.1.2.3.2. Face pictures. Control participants' performance decreased progressively as similarity between the target face and its distractor increased, just like their pattern of performance with pictures of cars. However, LR's pattern of results with faces was strikingly different from his performance with pictures of cars. First, although LR's overall performance did not differ significantly from normal controls ($p=0.08$), he was significantly impaired in accuracy for the three first levels of dissimilarity, the three easiest ones, that is 100% ($p<0.001$), 80% ($p<0.05$), and 60% ($p<0.05$) (Table 3). His accuracy rates were in the range of normal controls for the last two levels (see Table 3 and Fig. 4B). He was slowed down overall ($p<0.01$), and significantly slowed down relative to controls for the first four levels of dissimilarity, at 100% ($p<0.001$), 80% ($p<0.001$), 60% ($p<0.01$) and 40% ($p<0.01$). He performed in the normal range at the fifth level of dissimilarity – the most difficult one (see Table 3 and Fig. 4B). LR's regression slopes did not differ from controls, neither for accuracy rates ($t_6=0.116$, $p=0.91$), nor correct response times ($t_6=0.994$, $p=0.36$).

Altogether, these observations yet again contradict the account of prosopagnosia in terms of impairment in processing visually similar items (Faust, 1955; Damasio, Damasio, & Van Hoesen, 1982; Gauthier, Behrmann, & Tarr, 1999) and replicate the recent findings obtained with two other cases of acquired prosopagnosia (Busigny, Joubert et al., 2010; Busigny, Graf et al., 2010). Like these two cases, LR's slope of accuracy and RTs at discriminating visually similar pictures of cars was entirely normal. With faces, LR's decreased performance relative to controls was the largest when the faces to discriminate were clearly dissimilar, showing a very similar pattern of performance as the previous cases (albeit with a less severe impairment). This finding directly contradicts the view that prosopagnosia is due to a difficulty in processing items that are visually similar because under this hypothesis one would have expected LR's difficulties to rather increase more than controls as similarity increases. Admittedly, we cannot exclude that the absence of a difference for the most difficult visual discrimination level reflects a floor effect (the control participants performing relatively poorly with highly similar faces), even though there was still room for a decrease of performance even with highly similar faces (40% of dissimilarity: 79% of correct responses; 20% of dissimilarity: 66% of correct responses for normal participants) and increase of RTs.

If LR's prosopagnosia is not a problem at disambiguating items that are visually similar, alternative explanations need to be considered. In the next section, we directly test LR's holistic perception of individual faces.

3.2. Holistic perception of the individual face

3.2.1. Face inversion effect

Inversion is perhaps the most widely used transformation applied to face stimuli in the scientific literature, following the work of Yin (1969), in which it was found that this manipulation affected the recognition of faces much more than other mono-oriented object categories. While the reason(s) underlying the detrimental effect of face inversion continues to be a matter a debate in the literature

Table 2
LR' accuracy rates and response times for the experiment 2: Discrimination of visually similar pictures of cars. Standard deviations are provided in parentheses. *T*-values correspond to the modified single case *t*-test of Crawford and Howell (1998).

	Accuracy(%)				RTs (ms)			
	Controls	LR	*t*	*p (one-tailed)*	Controls	LR	*t*	*p (one-tailed)*
100% diff.	97.8 (3.24)	96.9	0.265	*0.40*	1271 (155)	1403	0.812	*0.22*
80%	95.8 (4.66)	100	0.859	*0.21*	1413 (232)	1366	0.193	*0.43*
60%	90.1 (6.42)	93.8	0.550	*0.30*	1527 (306)	1620	0.290	*0.39*
40%	83.1 (9.09)	84.4	0.136	*0.45*	1910 (426)	2612	1.571	*0.08*
20%	61.3 (14.43)	56.3	0.330	*0.37*	2807 (1273)	3067	0.195	*0.43*
Overall	85.6 (5.74)	86.3	0.116	*0.46*	1853 (529)	2014	0.290	*0.39*

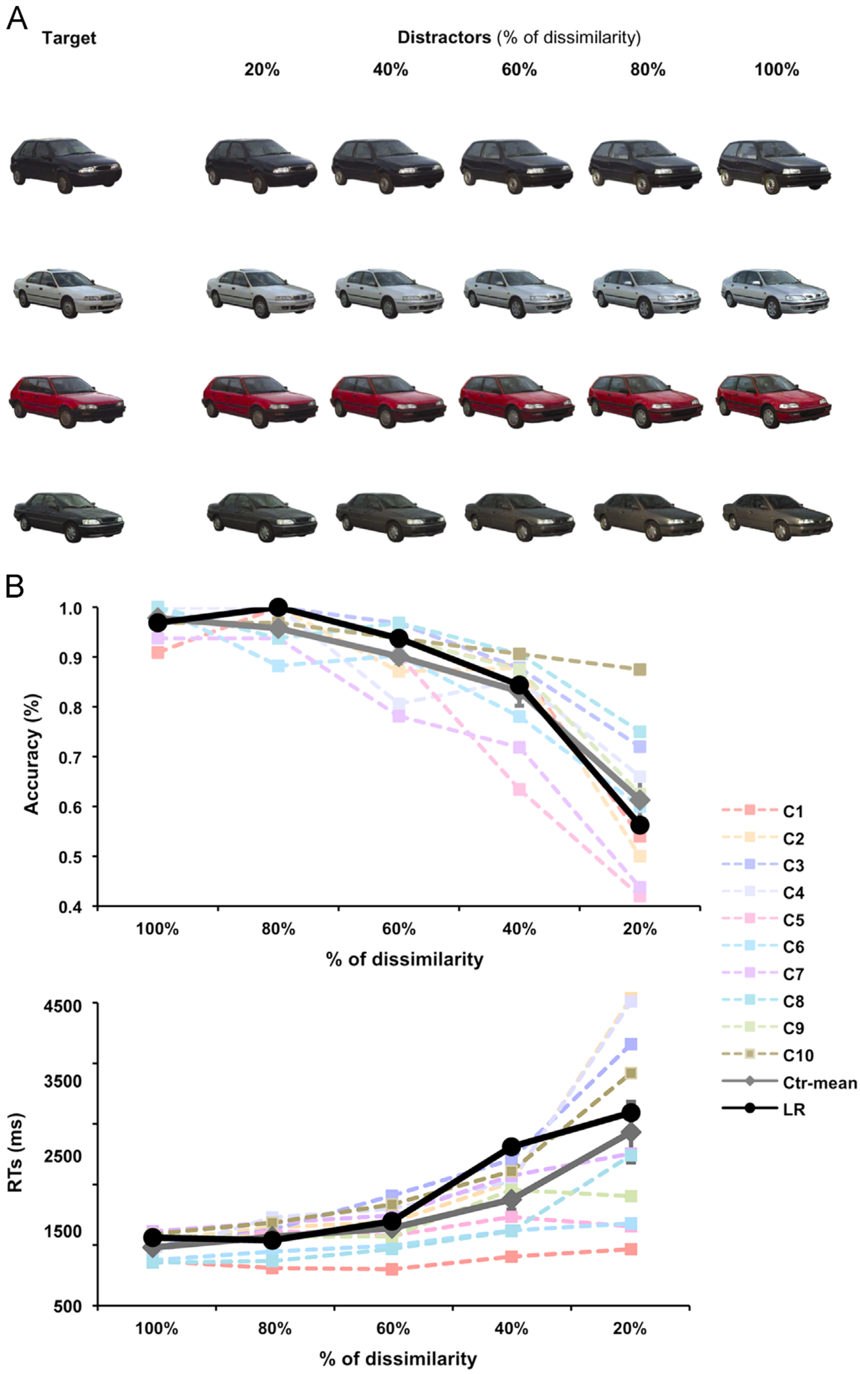

Fig. 3. Experiment 2: discrimination of visually similar items: Cars. (A) Examples of car stimuli. (B) Accuracy and response times of LR and controls for the car category. Error bars for controls indicate standard errors.

Table 3
LR' accuracy rates and response times for the experiment 2: Discrimination of gradually similar faces (*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$). Standard deviations are provided in parentheses. *T*-values correspond to the modified single case *t*-test of Crawford and Howell (1998).

	Accuracy(%)				RTs (ms)			
	Controls	LR	*t*	*p (one-tailed)*	Controls	LR	*t*	*p (one-tailed)*
100% diff.	99.5 (0.75)	90.6	11.314	*0.000****	999 (93)	1533	5.475	*0.000****
80%	98.1 (1.44)	93.8	2.847	*0.010**	1094 (122)	1715	4.853	*0.000****
60%	94.1 (3.19)	87.5	1.973	*0.040**	1174 (133)	1704	3.800	*0.002***
40%	79.1 (6.76)	78.1	0.141	*0.45*	1404 (187)	2252	4.324	*0.001***
20%	66.6 (11.30)	57.8	0.743	*0.24*	1921 (718)	2760	1.114	*0.15*
Overall	87.5 (3.64)	81.6	1.548	*0.08*	1278 (191)	1993	3.569	*0.003***

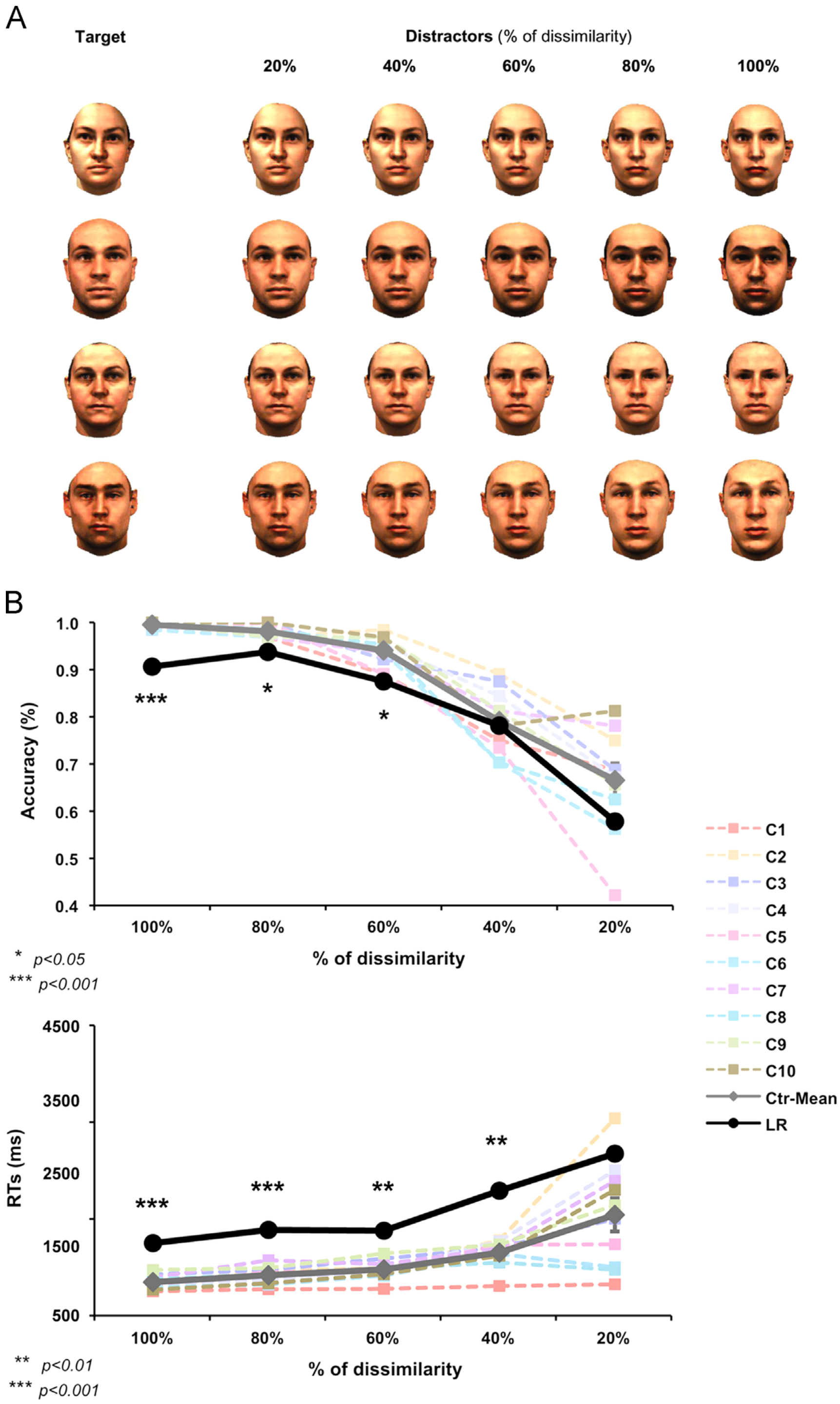

Fig. 4. Experiment 2: discrimination of visually similar items: Faces. (A) Examples of face stimuli. (B) Accuracy and response times of LR and controls for the face category. Error bars for controls indicate standard errors. Asterisks refer to the significance of the *t*-values provided by the modified *t*-test of Crawford and Howell (1998), performed between LR and controls.

(for recent reviews, see Rossion, 2008, 2009), most authors agree that inversion affects our ability to perceive a face holistically/configurally (Farah, Wilson, Drain, & Tanaka, 1998; Maurer, Le Grand, & Mondloch, 2002; Rossion, 2008, 2009). Several cases of prosopagnosia have been tested with upright and inverted faces (e.g., McNeil & Warrington, 1991; Farah, Wilson, Drain, & Tanaka, 1995; Marotta, McKeeff, & Behrmann, 2002; Riddoch et al., 2008). According to a recent review, the face inversion effect is present abnormally in cases of acquired prosopagnosia, being generally reduced or even abolished (Busigny & Rossion, 2010a).

Bukach et al. (2006) already tested LR with upright vs. inverted faces in a sequential-matching paradigm. However, the stimuli were also modified in terms of spatial relations between parts (position of the eyes and the mouth) and the parts themselves (identity of the eyes and the mouth). The authors reported a decrease of sensitivity to the eye region, as already mentioned, but there was no direct comparison of LR's performance for inverted faces vs. upright faces relative to controls, so that the presence and magnitude of LR's inversion effect for faces remain unclear. Moreover, there were no other visual stimuli included in the paradigm to test whether a potential disruption of performance by inversion would be specific to faces. Here, we conducted two new experiments dedicated to assess face inversion effect in LR, the first experiment (Experiment 3) simply comparing results in the Benton Face Recognition Test (BFRT) in the upright and the inverted orientations, the second experiment (Experiment 4) comparing inversion effect for faces to inversion effect for another class of mono-oriented stimuli (cars).

3.2.2. Experiment 3. BFRT upright and inverted

3.2.2.1. Material and procedure. LR was administered an electronic version of the BFRT, with faces in upright (day 1) and inverted (day 2) orientations. Control participants also performed the upright orientation first and the inverted orientation one day later.

3.2.2.2. Control participants. Ten healthy controls were tested (mean age: 56.4; SD: 7.06).

3.2.2.3. Results. There was a large inversion effect for control participants (17% on average, $t_9=10.468$, $p<0.001$) (Fig. 5). In contrast, there was no significant difference between upright and inverted faces for LR ($Chi2_1=0.831$, $p=0.18$) (Fig. 5). LR performed lower than control participants for upright faces ($t_9=2.456$, $p<0.05$), while he performed in the normal range for inverted faces ($t_9=-1.546$, $p=0.08$). Note that LR's performance was clearly above chance level (18/54=33%) in the test, so that this absence of inversion effect cannot be attributed to a floor effect.

Importantly, these results also show that LR is not only impaired at processing faces when there is a temporal delay between the items to match/discriminate (as suggested in Bukach et al., 2006), but that he may also have difficulties at matching/discriminating faces presented simultaneously.

Regarding RTs, controls performed the test significantly faster for upright (mean: 5min47″; SD: 80″) than inverted faces (mean: 7min41″, SD: 148″, $t_9=3.284$, $p<0.01$). Compared to controls, LR was slowed down at both orientations (upright: 10min44″, $t_9=3.540$, $p<0.01$; inverted: 13min28″, $t_9=2.235$, $p<0.05$). He was also slightly faster in the upright condition. However only the total time to perform the test was calculated for both orientations. In consequence, we were not able to calculate and compare response times on correct trials as we did in the other experiments, and as will be done in the following experiment.

3.2.3. Experiment 4. Delayed matching of faces and cars upright and upside-down

3.2.3.1. Material and procedure. This second experiment aimed at comparing the inversion effect for faces to the effect for a highly familiar non-face category, namely pictures of cars. It is known that non-face categories, in particular car pictures, also elicit

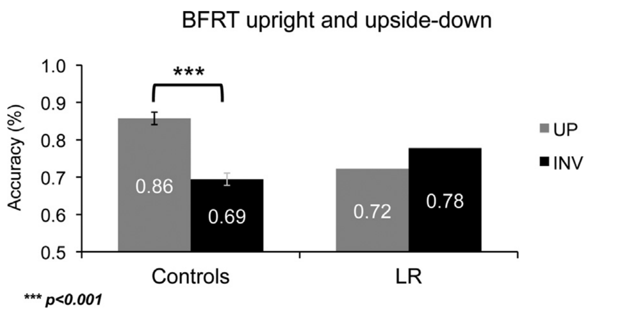

Fig. 5. Experiment 3: Benton Face Recognition Test in upright and the inverted orientations. Accuracy rates of LR and controls. Error bars for controls indicate standard errors. Asterisks refer to the significance of the *t*-value provided by the paired sample *t*-test performed between upright and inverted orientations in controls.

inversion costs in matching or recognition tasks, but of much smaller magnitude than for faces (e.g. Yin, 1969; Scapinello & Yarmey, 1970; Valentine & Bruce, 1986; Leder & Carbon, 2006; Robbins & McKone, 2007; Rossion & Curran, 2010). In this second experiment, we used a delayed two-alternative forced choice matching task (Experiment 4 in Busigny & Rossion, 2010a). One full front and one 3/4 profile grayscale photographs of 36 faces (eighteen females) and 36 cars were used. The target picture was always a full-front picture, and the probe a 3/4 profile picture. Each photograph was presented in upright and inverted orientations. Participants had to choose which of two 3/4 profile probes was the same identity as the full-front target presented earlier by pressing a keyboard key (left or right) corresponding to the location of the target face (or car). Each trial began with a white screen (1000 ms), followed by the target (2000 ms), an ISI (1000 ms), and the probe screen (until response). Each new trial was initiated after the response of the participants. The experiment was divided into two blocks of 72 randomized trials preceded by seven practice trials. In total, 72 trials were used for both orientations (36 per condition). The size of the stimuli subtended approximately $7.1° \times 5.7°$ for faces and $5° \times 7.8°$ for cars, presented on a white background.

3.2.3.2. Control participants. Ten healthy controls were tested (mean age: 57.9; SD: 8.02).

3.2.3.3. Results and discussion. Control participants had a large face inversion effect on accuracy ($t_9=11.558$, $p<0.001$) and on correct RTs ($t_9=6.553$, $p<0.001$). For upright faces, LR performed lower than controls ($t_9=1.902$, $p<0.05$) and he was significantly slowed down ($t_9=4.466$, $p<0.01$). With inverted faces, his performance was within the normal range for accuracy ($t_9=0.291$, $p=0.39$), but he was also slowed down relative to controls ($t_9=2.985$, $p<0.01$) (Fig. 6A and B). Importantly, there was no face inversion effect for LR, neither in accuracy ($Chi2_1=0.799$, $p=0.19$), nor in correct RTs ($t_{50}=0.327$, $p=0.37$; mean ± SD RT computed across trials: upright: 3368 ± 2326 ms; inverted: 3564 ± 1884 ms).

For pictures of cars, control participants did not show a significant inversion effect in accuracy ($t_9=1.525$, $p=0.08$) but they did so in correct RTs ($t_9=3.04$, $p<0.01$). LR's performance did not differ from controls for upright ($t_9=0.494$, $p=0.32$) and inverted cars ($t_9=0.289$, $p=0.39$). Just like the control participants, he did not show a significant car inversion effect in accuracy ($Chi2_1=1.530$, $p=0.11$) (Fig. 6A). Regarding RTs, LR did not differ from controls at any orientation (upright cars: $t_9=0.214$, $p=0.42$; inverted cars: $t=0.057$, $p=0.48$). Hence, like normal controls, LR had a significant inversion effect in correct RTs for cars ($t_{67}=10.436$, $p<0.01$; mean ± SD RT computed across trials: upright: 1444 ± 744 ms; inverted: 1759 ± 927 ms) (Fig. 6B).

We also computed an index of the 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 face inversion effect for LR and each control participant. First, we computed the inverse efficiency (average response times of the correct trials divided by accuracy; Townsend & Ashby, 1983). Next, we calculated the percentage of the face inversion effect for each participant using the following formula: (Inverse efficiency upright − Inverse efficiency inverted)/(Inverse efficiency upright + Inverse efficiency inverted). We calculated these indexes of inversion effects for both cars and faces. The indexes indicate that LR was the only participant who showed a tendency for a larger inversion index for cars than faces (Fig. 6C). In contrast, all normal participants had a larger inversion effect for faces than for cars. Notably, LR's car inversion index (12.7%) was in the normal (upper) range (mean: 5.9%, SD: 4.87; $t_9=1.331$, $p=0.11$), while his face inversion index (7.1%) was significantly

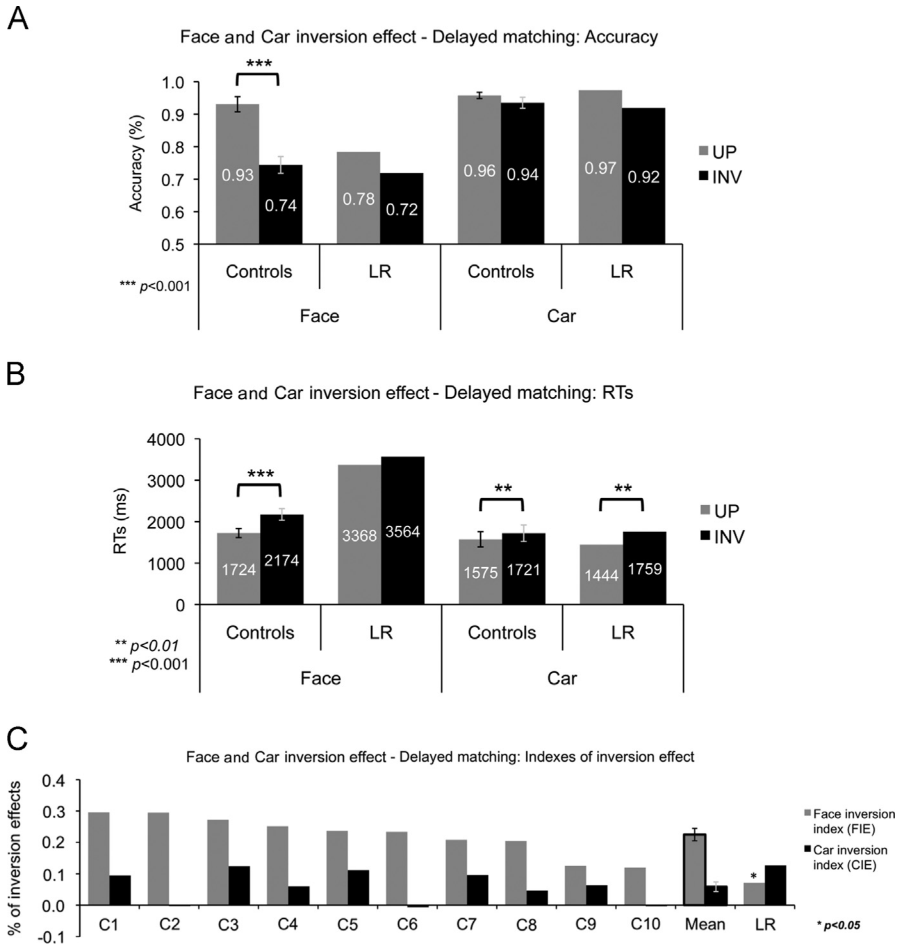

Fig. 6. Experiment 4: Delayed matching of faces and cars upright and upside-down. (A) Accuracy rates for LR and controls. (B) Response times on correct trials for LR and controls. (C) Individual indexes of inversion calculated with the following formula: (Upright − Inverted)/(Upright + Inverted). Error bars for controls indicate standard errors computed across subjects. In (A and B), asterisks refer to the significance of the *t*-values provided by the paired sample *t*-tests for controls and the independent sample *t*-test for LR. In (C), the asterisk refers to the significance of the *t*-value provided by the modified *t*-test of Crawford and Howell (1998) performed between LR and controls.

below normal controls (mean: 22.5%, SD: 6.23; $t=2.357$, $p<0.05$). Moreover, results from applying the Revised Standardized Difference Test (Crawford & Garthwaite, 2005), to compare a single patient's discrepancy with the control sample, showed that LR had a profile significantly different from controls ($t_9=2.802$, $p<0.05$). While the controls presented with a stronger inversion effect for faces than for cars, LR did not show this dissociation.

In conclusion, LR's profile of performance was comparable to normal observers when matching pictures of upright cars across viewpoint changes. In contrast, LR performed lower than controls when matching faces. This observation reinforces the selectivity of his impairment for faces. In addition, LR did not present with a normal effect of inversion for faces. Since his inversion effect for photographs of cars was in the normal range, this absence of an inversion effect cannot be explained by a general factor. Hence, LR's acquired prosopagnosia seems to affect primarily a process that is specific to upright faces. These observations are in line with the absence of inversion effect for the prosopagnosic patient PS tested extensively with upright and inverted faces (Busigny & Rossion, 2010a), as well as for other such patients (e.g., McNeil & Warrington, 1991; Boutsen & Humphreys, 2002; Delvenne et al., 2004; Busigny et al., 2010b).

3.2.4. *Experiment 5. whole-to-part effect*

3.2.4.1. Rationale. We aimed to provide more direct evidence for the patient LR's deficient holistic processing of individual faces. A paradigm that is classically used is the *face superiority effect* (Tanaka & Farah, 1993), also called the *whole-part advantage* (e.g., Delvenne et al, 2004). It refers to the superior discrimination of two whole faces differing by one part (e.g., the eyes) in comparison to the discrimination of these parts when they are shown in isolation. In other words, the discrimination of the diagnostic part is facilitated by the presence (and correct organization) of the remaining facial parts. This effect is thought to reflect the fact that a change of one diagnostic part affects the whole face, thus making the discrimination easier (Tanaka & Farah, 1993). Different kinds of whole-part advantage paradigms have been used with prosopagnosic patients: two-alternative forced choice matching tasks (Davidoff & Landis, 1990; Delvenne et al., 2004; Wilkinson et al., 2009) or variants with "Thatcherized" faces (Boutsen & Humphreys, 2002; Riddoch et al., 2008). All these studies showed that patients with acquired prosopagnosia were relatively impaired at showing an advantage for processing whole faces vs. isolated parts.

Here we assessed this effect in a delayed face matching task, as in most studies with normal observers (e.g., Michel, Caldara, & Rossion, 2006a; Goffaux & Rossion, 2006). We presented wholes and parts of faces preceded by whole faces, and we completed the paradigm by also including trials in which the first stimulus could be part of a face followed by wholes or parts of faces (see Ramon et al., 2010). The diagnostic cue for analysis was the eyes, but there were foil trials for mouth and nose. The prediction was that, for normal observers, the performance would be better (higher accuracy, slower RTs) when the format of the encoding (target) stimuli and format of the subsequently presented test (probe) stimuli were identical. That is, the conditions "part-part" and "whole-whole" should be associated with superior performance as compared to "part-whole" and "whole-part", respectively. Thus, the effect would not necessarily be a whole/part advantage, but a demonstration that the processing of facial parts, at least in normal participants, is influenced by the presence of the other features (see Leder & Carbon, 2005).

3.2.4.2. Material and procedure. Thirty grayscale full-front pictures of unfamiliar faces (half female) posing with a neutral expression, cropped without external features and free of facial hair or glasses served as stimuli. Using Adobe Photoshop, we created 20 eye-foils by swapping the eye region amongst 20 of the original faces. The remaining ten original faces were used to generate five nose-foils and five mouth-foils using the same feature swapping procedure. Isolated features (eyes, nose or mouth) were generated by isolating the relevant feature, resulting in a total of 30 feature stimuli (20 isolated eyes, five noses, five mouths). Nose and mouth foil face parts and whole faces were used as catch trials (one third of the trials, 40/120) in the experiment to avoid participants exclusively focusing on the eyes, and these trials were not analyzed (as in our previous studies with this paradigm: e.g., Michel et al., 2006a; Ramon et al., 2010).

The task was delayed two-alternative forced choice identity matching, as described previously in Ramon et al. (2010) and Busigny et al. (2010a). Trials began with a target face stimuli presented centrally for 2000 ms. Following a blank screen of 500 ms, two juxtaposed probe stimuli remained on the screen until a response was made. Participants were instructed to select the probe that matched the target stimulus by pressing the key corresponding with probe location (right versus left) on the screen. The next trial started 1000 ms after each response. The target stimulus was either an original face (whole-whole and whole-part conditions) or a single part (part-part and part-whole conditions). Each target item was slightly larger in size than the probe stimuli.

In the *whole display* condition, the probes were whole faces, one identical to the target, the other one (i.e., the foil) differing from the target by a single part (eyes in experimental trials, nose or mouth in catch trials). In the *part display* condition, the probes depicted isolated face parts (eyes in experimental trials, nose or mouth in catch trials) (see Fig. 7A). There were 40 trials per experimental condition, and 160 trials in total. Each target and probe stimulus appeared four times. The location of foil stimuli (right versus left) was counterbalanced. Eighty catch trials (mouth and nose whole and part foils) were added, giving a total of 240 (four blocks of 60 trials). Trial order was at random and varied for each participant. Six practice trials were completed before the experiment commenced. The target stimulus subtended $5 \times 6^{\circ}$ of visual angle, while size of the subsequently presented probes differed depending on probe type (whole faces: $4.1 \times 4.1^{\circ}$; eye feature stimuli: $0.7 \times 4^{\circ}$; nose features: $1.4 \times 1.4^{\circ}$; mouth features: $1 \times 2^{\circ}$). All stimuli were presented on a gray background.

3.2.4.3. Control participants. Ten healthy controls were tested (mean age: 59.4; SD: 6.8).

3.2.4.4. Results and discussion. Normal controls showed a significant advantage in the *whole-whole* as compared to the *whole-part* condition ("Whole-part advantage") with respect to accuracy ($t_9=2.587$, $p<0.05$) and correct RTs ($t_9=12.852$, $p<0.001$) (Fig. 7B & C). They also showed a significant "Part-whole disadvantage" when comparing the *part-part* and the *part-whole* conditions, both in terms of accuracy ($t_9=3.399$, $p<0.01$), and correct RTs ($t_9=5.387$, $p<0.001$). These results show that the control participants are better and faster when the encoding and retrieval face context is the same.

In contrast, LR showed no difference between the *whole-part* and the *whole-whole* conditions, neither in accuracy nor in correct RTs ($t_{60}=0.684$, $p=0.25$; mean $\pm$ SD RT computed across trials: whole-whole: 2103 ± 684 ms; whole-part: 2218 ± 639 ms) (Fig. 7B & C).

Considering the *part-part* and the *part-whole* conditions, LR showed no significant effect in accuracy ($\text{Chi2}_1=2.057$, $p=0.08$), but there was a significant difference in the expected direction in RTs ($t_{64}=2.749$, $p<0.01$; mean $\pm$ SD RT computed across trials: part-part: 1567 ± 361 ms; part-whole: 1970 ± 771 ms) (Fig. 7C).

Indexes were computed using the same formula that was used for the inversion effect (see above). Thus we calculated an index for the condition in which the whole face is presented first (Inverse efficiency whole-part − Inverse efficiency whole-whole)/(Inverse efficiency whole-part + Inverse efficiency whole-whole) and for the condition in which the part is presented first (Inverse efficiency part-whole − Inverse efficiency part-part)/(Inverse efficiency part-whole + Inverse efficiency part-part). In the *whole display* condition, each single control participant obtained a high index of whole-part advantage (mean = 16.7%, SD: 6.86), but this was not the case for LR, who obtained an index close to zero (2.66%), significantly lower than the controls ($t_9=1.954$, $p<0.05$) (Fig. 7D). In the *part display* condition, each participant showed a high index of part-whole disadvantage (mean = 14.7%, SD: 4.91). This time, LR did not show a significantly reduced effect compared to controls (LR: 15.4%, $t_9=0.150$, $p=0.44$) (Fig. 7E).

In conclusion, normal controls show both a whole-part advantage and a part-whole disadvantage, while LR shows only the second effect. That is, he does not perform better at discriminating a part embedded in a whole face than when presented in isolation. However, when he is presented with a face part at encoding, he recognizes the part better if it is isolated than when it is embedded in a whole face. This effect could be the consequence of residual face holistic processing. This residual face holistic processing could be insufficient to produce a positive effect (an advantage of the face configuration), but could be sufficient to produce a negative effect (the disadvantage of supplementary facial information). We will come back to this issue in the discussion section.

3.2.5. Experiment 6. Composite face effect: top composite (alignment × identity)

3.2.5.1. Rationale. The composite face effect was originally described by Young, Hellawell, and Hay (1987) as the difficulty to identify the top half (or bottom half) of a famous face when it is aligned with the bottom half (or top half) of another person. It is thought to reflect the fact that one half of a face cannot be perceived in isolation, but is integrated into a whole face representation. This paradigm was later applied to the matching of individual unfamiliar faces, in which two identical top halves of faces are perceived as being slightly different if they are aligned with distinct bottom halves (e.g., Hole, 1994; Le Grand, Mondloch, Maurer, & Brent, 2004; Michel, Rossion, Han, Chung, & Caldara, 2006b; Goffaux & Rossion, 2006; Rossion, 2013 for a review). As mentioned in the introduction, LR has already been tested with composite faces by Bukach et al. (2006), who concluded that he did not differ from normal controls at this task. However, critically, these authors did not include misaligned face halves in their paradigm, and thus merely tested a Stroop-like congruency/interference effect (whether an irrelevant face half interferes with a matching/discrimination decision on target face half), not a composite face effect (see Rossion, 2013).

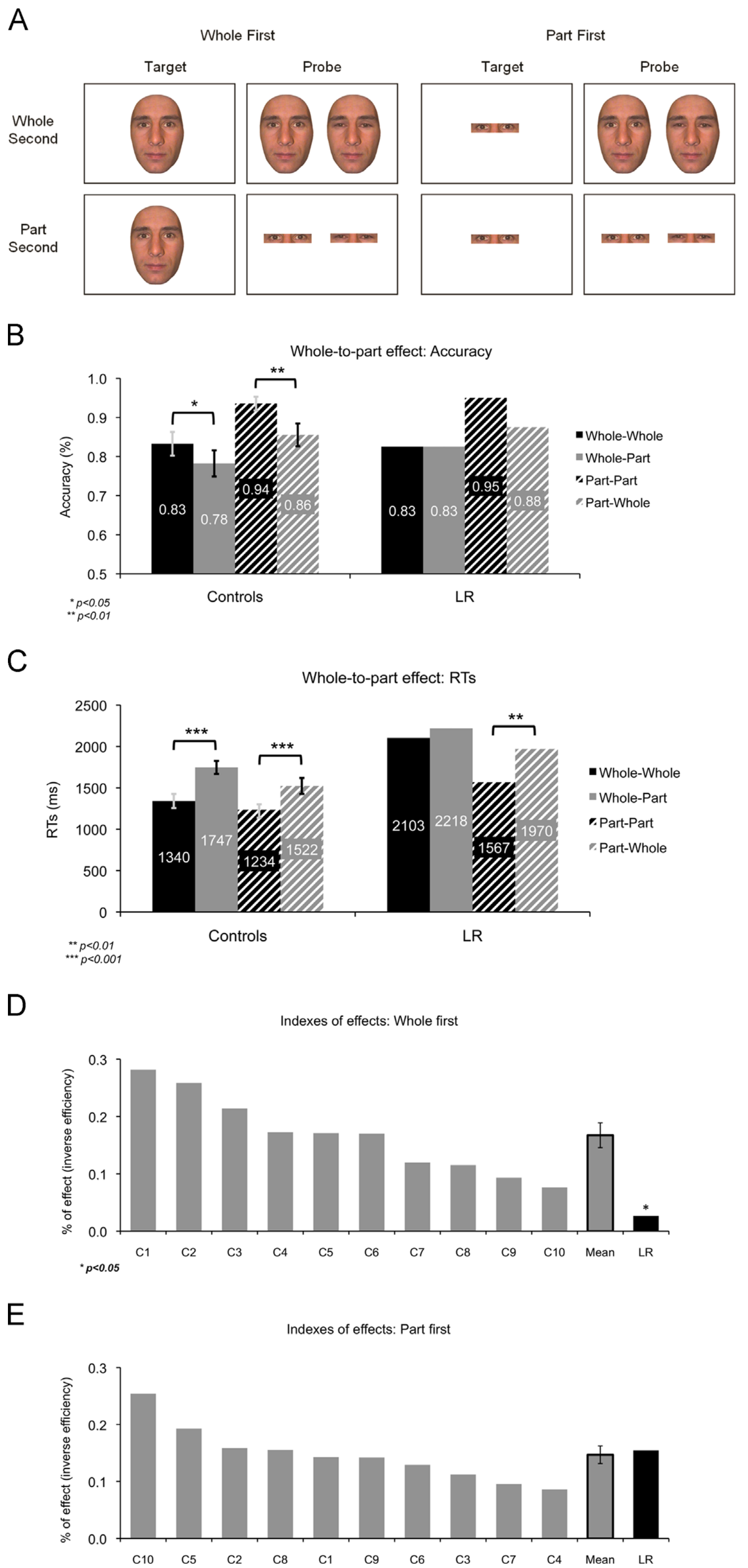

Fig. 7. Experiment 5: Whole-to-Part effect. (A) Examples of stimuli in each condition. (B) Accuracy rates for LR and controls. (C) Response times on correct trials for LR and controls. (D) Individual indexes of the whole-part advantage calculated with the following formula: (whole-part − whole-whole)/(whole-part + whole-whole). (E) Individual indexes of part-whole disadvantage calculated with the following formula: (part-whole − part-part)/(part-whole + part-part). Error bars for controls indicate standard errors. In Figs. 7B and C, asterisks refer to the significance of the *t*-values provided by the paired sample *t*-tests for controls and the independent sample *t*-test for LR. In (D), the asterisk refers to the significance of the *t*-value provided by the modified *t*-test of Crawford and Howell (1998), performed between LR and controls.

Given these observations, we used the last experiment described in Ramon et al. (2010), experiment 5; see also Busigny et al., 2010a, experiment 24), in which there were four critical conditions for which the top half of the faces was the same (Aligned/Same Bottom; Aligned/Different Bottom; Misaligned/Same Bottom; Misaligned/Different Bottom). For normal controls, we expected a composite effect, that is an effect of *alignment* (misaligned trials performed better than aligned trials), which should be observed only when the bottom halves differ between the faces to match. In contrast, this effect was not expected for LR.

3.2.5.2. Material and procedure. The stimuli used in this experiment were full-front color pictures of 23 unfamiliar faces (neutral expression, 16 female, no glasses or facial hair) that were cropped so that neither hair nor external features were depicted. The resulting faces, subtending approximately 160 pixels in width and 230 pixels in height, were fitted onto a white background. Using Adobe Photoshop, the original faces were separated by inserting a 1.76 mm gap located above the nostril upper limit. The gap was used so that the border separating the top and bottom halves could be well identified, even in the aligned condition (see Rossion, 2013 for the rationale for using such a gap). Each original face was transformed into two stimuli: the first one ("original") differed from the original merely by the inserted gap (Same Top/Same Bottom), the second one ("composite") had a given top part combined with a different bottom part from a randomly selected other face (i.e., a composite face). Misaligned versions were created by laterally offsetting the lower parts so that the top part's right edge of the nose was aligned with the bottom part's left side of the nose.

Participants performed a two-alternative forced choice decision task (see Ramon et al., 2010; Busigny et al., 2010a). Each trial involved the consecutive presentation of two stimuli (both either aligned or misaligned), which had to be judged with regard to the identity of the top part (i.e., same or different) (see Fig. 8A). There were four possible trials requiring a "same" response: the original face paired with itself ('Aligned/Same Bottom'; 'Misaligned/Same Bottom') and different composite faces that had the same top half but a different bottom half ('Aligned/Different Bottom'; 'Misaligned/Different Bottom'). There were also real "different" trials, in which a face was paired with another randomly selected face so that both face halves were different (see Rossion, 2013; Figure 26 for a display of this paradigm). This paradigm was used in several previous studies and is highly sensitive to disclose a composite face effect in normal participants (e.g., Ramon et al., 2010; Busigny et al., 2010b).

Trials started with a fixation cross presented centrally for 300 ms. Following a 200 ms blank, a target face was presented for 600 ms. After a 300 ms ISI, the probe face appeared until a response was provided. The next trial was initiated 1000 ms after a given response. In order to restrict the possibility of participants engaging in comparing merely a specific location of the display while performing the matching task, the target and sample faces appeared at slightly different screen locations. Participants were asked to attend only to the top parts and to respond whether these were the same or different (by pressing a right or left key, respectively). In line with previous studies (e.g., Goffaux & Rossion, 2006; Michel et al., 2006b), trials in which both halves were different were used only as catch trials, and not considered in the analysis (Rossion, 2013). The experiment consisted of a total of 138 trials, which were divided into two blocks of equal length. There were 92 "same" trials (23 per condition) and 46 "different" trials (23 per condition). Prior to the beginning of the experiment, participants completed four practice trials. Aligned stimuli subtended approximately $5.7 \times 3.8^{\circ}$ of visual angle and misaligned stimuli $5.7 \times 5.2^{\circ}$.

3.2.5.3. Control participants. Ten healthy controls were tested (mean age: 62; SD: 6.68).

3.2.5.4. Results. The data of age-matched normal controls are illustrated in Fig. 8(B & C). The ANOVA for accuracy rates showed a significant main effect of *alignment* ($F_{(1,9)}=5.000$, $p<0.05$), and a significant main effect of *identity* of the bottom half ($F_{(1,9)}=7.653$, $p<0.05$). Moreover, there was a significant interaction between the two factors ($F_{(1,9)}=4.048$, $p<0.05$): performance decreased only when the two parts were aligned *and* when the bottom face half was different. The ANOVA for RTs showed a main effect of *alignment* ($F_{(1,9)}=3.844$, $p<0.05$), and a main effect of *identity* of the bottom half ($F_{(1,9)}=9.985$, $p<0.01$). Most importantly, in line with the results for accuracy, there was a highly significant interaction between the two factors ($F_{(1,9)}=26.963$, $p<0.001$). These findings are a hallmark of holistic face perception for control participants.

A bootstrap procedure with 10,000 iterations for each condition on the accuracy rates of LR indicated the same profile as the normal controls: lower performance for the aligned stimuli with different bottom halves ('Aligned/Different Bottom' trials, $M=0.78$; CI=[0.6087, 0.95652]) than for all other conditions ($p<0.01$). Performance in both misaligned conditions was at ceiling ($M=1$; CI=[1, 1]) and did not differ significantly from the aligned condition with same bottom halves ('Aligned/Same Bottom' trials, $M=0.96$; CI=[0.86957, 1]; $p=0.40$) (Fig. 8B). However, in correct RTs, LR's profile was different. He showed no significant main effect of *alignment* ($F_{(1,85)}=2.115$, $p=0.08$), and only a main effect of *identity* ($F_{(1,85)}=6.905$, $p<0.01$). There was no interaction between the two factors ($F_{(1,85)}=0.272$, $p=0.30$) because LR showed an unexpected increase of RTs in the 'Misaligned/Different Bottom' condition (Fig. 8B & C).

To compare LR's magnitude of composite effect with the controls, indexes were computed individually by using the formula: ('Aligned/Same Bottom' – 'Aligned/Different Bottom') – ('Misaligned/Same Bottom' – 'Misaligned/Different Bottom'). As in our previous study (Busigny et al., 2010b), given the inter-subject variance in the magnitude of the effect in accuracy rates, the indexes were calculated on the normalized correct response times. There was a high index of composite effect (mean = 18.39%, SD: 5.7) for every participant. LR's composite face effect index was in the lower range but did not differ from controls (LR: 11.08%; $t=1.223$, $p=0.13$) (Fig. 8D). However, a careful look at the data suggests that LR has a different profile of response in this task than normal controls. Indeed, while LR's performance was influenced by the identity of the bottom half similarly to the normal controls in the aligned condition (LR: 33.5%, controls mean: 19.08%, SD: 9.45, $t_9=1.455$, $p=0.09$) (Fig. 8E), he also showed an influence of the bottom half in the misaligned condition (LR: 22.4%), contrary to normal controls (mean: 0.68%, SD: 6.44; $t_9=3.216$, $p<0.01$) (Fig. 8F).

Interestingly, these results do not contradict the results obtained by Bukach et al. (2006; Experiment 2), who reported that the identity of the bottom half of the face influenced LR's judgment on the top half. However, thanks to the inclusion of misaligned trials in the present study, a necessary baseline to measure the composite face effect (Rossion, 2013), we found that this influence generalizes to misaligned trials to some extent only for LR, leading to an uncharacteristic profile of response. This influence may be due to LR's well-documented tendency to use the lower part of the face, the mouth in particular, to match faces (Bukach et al., 2006, 2008). Importantly, such a strategy cannot be associated with preserved holistic processing.

3.2.6. Experiment 7. Gaze contingent individual face discrimination

3.2.6.1. Rationale. Gaze-contingently revealing/masking a portion of the visual field in a face matching task provides a way to

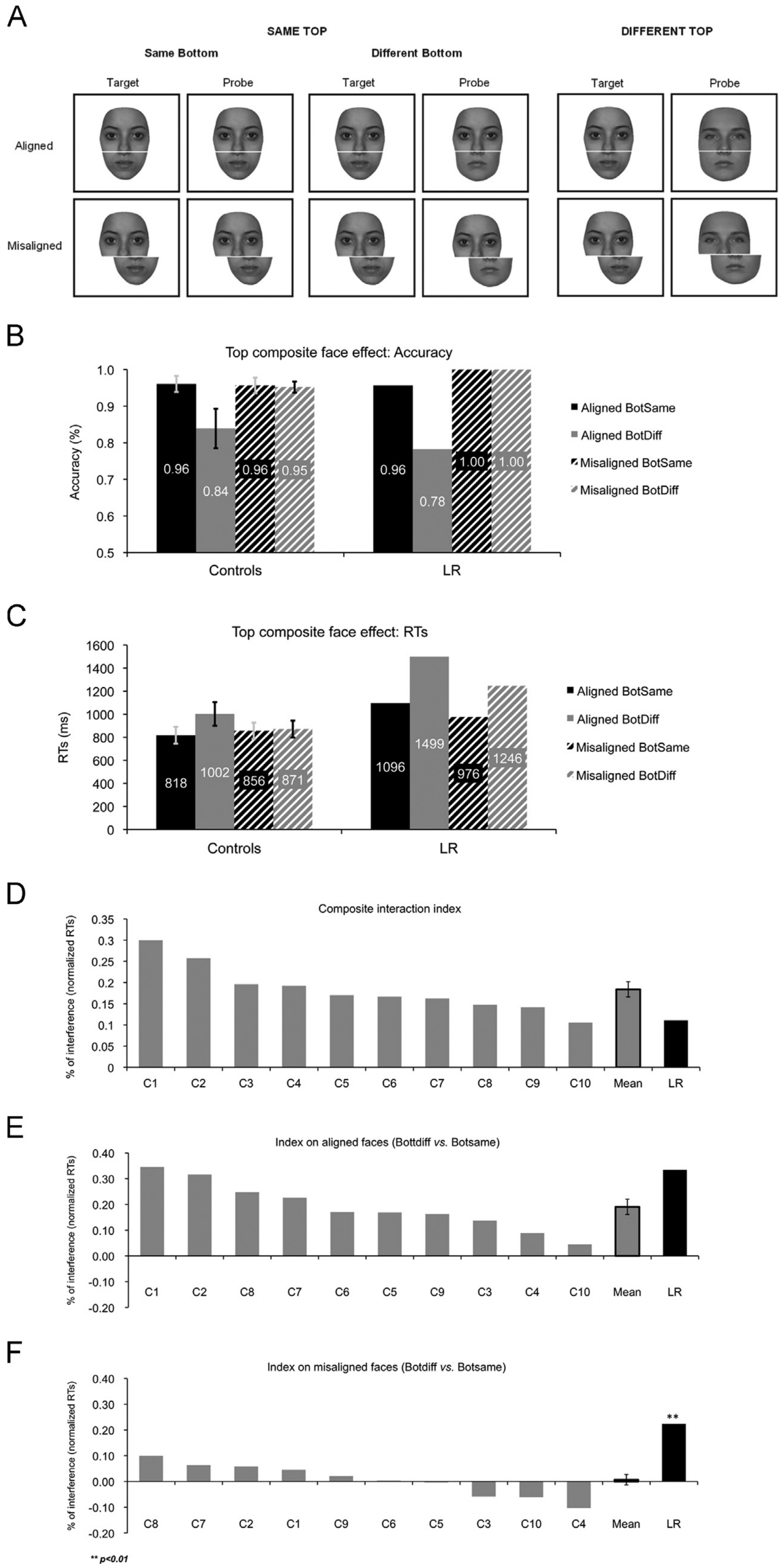

Fig. 8. Experiment 6: Composite face effect. (A) Examples of stimuli in each condition. (B) Accuracy rates for LR and controls in the four conditions for which the top half is the same. (C) Response times on correct trials for LR and controls (LR′ variance computed on trials is: 'aligned/same bottom': 1096 ± 543; 'aligned/different bottom': 1499 ± 589; 'misaligned/same bottom': 976 ± 246; 'misaligned/different bottom': 1246 ± 689). (D) Indexes of composite effect calculated with the following formula: ('aligned/same bottom' – 'aligned/different bottom') – ('misaligned/same bottom' – 'misaligned/different bottom'). (E) Indexes of the composite effect for the aligned trials calculated with the following formula: 'aligned/same bottom' – 'aligned/different bottom'. (F) Indexes of the composite effect for the misaligned trials calculated with the following formula: 'misaligned/same bottom' – 'misaligned/different bottom'. Error bars for controls indicate standard errors. In (F), asterisks refer to the significance of the t-value provided by the modified t-test of Crawford and Howell (1998), performed between LR and controls.

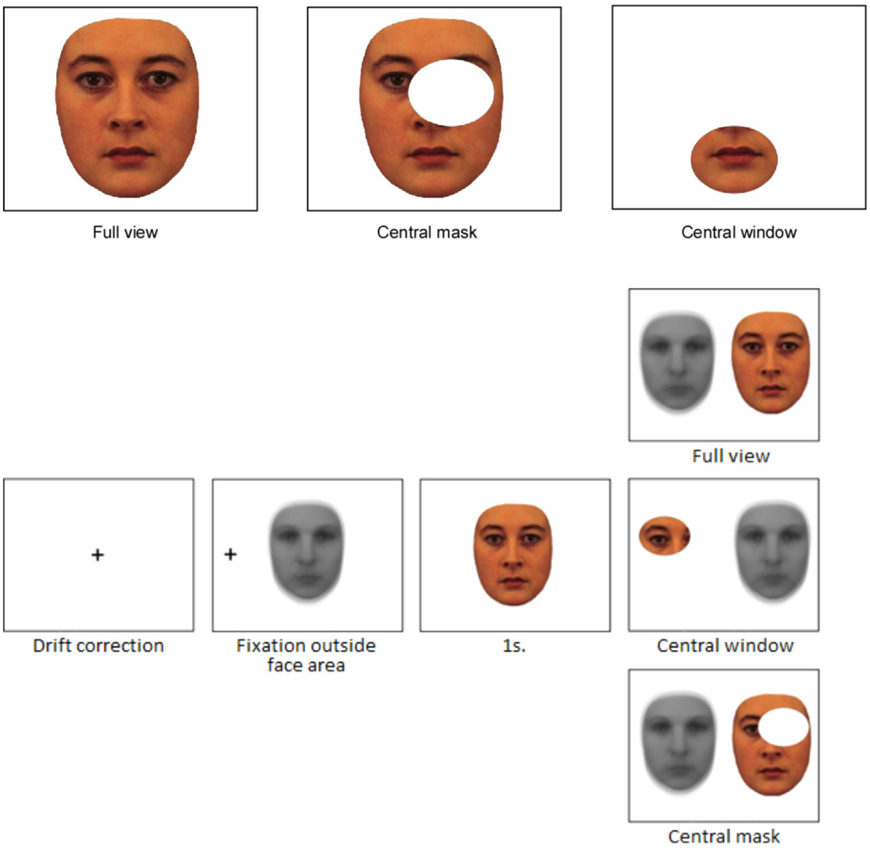

Fig. 9. Experiment 7: Gaze-contingent individual face discrimination (from Van Belle et al., 2010a). (A) Full view: the whole face is visible, central mask: only the non-fixated part of the face is visible, central window: only the fixated area of the face is visible. (B) experimental design: drift correction was followed by a fixation outside of the face area, a 1 s presentation of the reference face and two faces side by side until response.

selectively impair holistic or analytical processing. In a 'window' condition, only the fixated part is visible in a gaze-contingent window, preventing perception of multiple parts in the face at once, and impairing holistic perception. On the contrary, a mask condition, in which a mask covers the fixated part only, impairs analytical perception by preventing the use of highly detailed foveal information necessary for analytical processing (Fig. 9). This method demonstrated impairment in holistic face perception in two cases of acquired prosopagnosia: PS (Van Belle et al., 2010a) and GG (Van Belle et al., 2011). Compared to full view, PS' and GG's performance was almost unaffected when they could see only one part of the faces at a time (window condition), while they were largely impaired when the whole face but the fixated part was visible (mask condition). These findings were opposite to the observations made on normal controls. Gaze-contingency was also used to show that the face inversion effect increases in the mask condition and decreases in the window condition, reinforcing the link between these manipulations and the selective disruption of holistic vs. analytical processing (Van Belle, de Graef, Verfaillie, Rossion, & Lefèvre, 2010b).

Here, if LR has difficulties with holistic perception of individual faces, we expect his performance to differ from that of the control participants, especially in the mask condition.

3.2.6.2. Material and procedure. The methods are similar to the recent study of Van Belle et al. (2011) and will be briefly described here. For this experiment we used a stimulus set of 10 male and 10 female faces (KDEF database, Lundqvist, Flykt, & Ohman, 1998) with a height of 15°, from which the external features were cropped but head shape was largely preserved. A drift correction with a central fixation cross was followed by a centrally presented face. After 1 s, this reference face was replaced by two faces presented side-by-side, with a distance between the faces' inner borders of approximately 10°. The participant's task was to indicate which of the two faces corresponded to the reference face by pressing the assigned left or right key on the keyboard. The faces were randomly combined in pairs of two males or two females.

Participants could freely explore the side-by-side presented faces. In one third of the trials the faces were completely visible (full view). In another third of the trials, however, a gaze contingent mask covered the fixated feature in the central part of the visual field (mask condition). In the remaining third of the trials only the fixated feature in the central part of the visual field was visible through a limited spatial window (window condition) (Fig. 9).[1] The elliptical window and mask were $6 \times 5°$. During the exploration of the pair of faces, the face that was not fixated was replaced by a grayscale average of all faces in order to provide an equal reference frame for saccade planning, and an equal amount of information from the non-fixated face in all viewing conditions (Fig. 9). There were 75 trials per viewing condition, resulting in a total of 225 trials, presented in 5 blocks of 45 trials each. Viewing condition order was randomized across trials.

3.2.6.3. Control participants. Seven healthy controls were tested (mean age: 57; SD: 2.93).

[1] Movies of the gaze-contingency experiment as performed by the patient PS in a previous study are available at http://face-categorization-lab.webnode.com/pictures/.

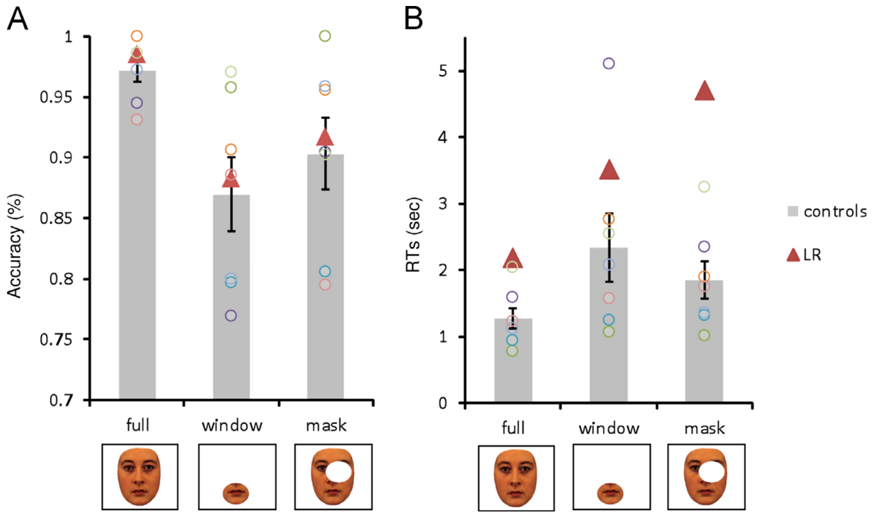

Fig. 10. Experiment 7: Gaze-contingent individual face discrimination. (A) Accuracy rates for LR and controls, including individual participants' performance. (B) Response times on correct trials for LR and controls, including individual participants' performance. Error bars indicate standard errors.

3.2.6.4. Results. Control participants showed a main effect of *viewing condition* on accuracy ($F_{(2,\ 12)}=6.51$, $p<0.05$). Individual contrasts were Tukey corrected for multiple comparisons (two-tailed). Compared to full view ($M=0.97$), accuracy significantly decreased with a window ($M=0.87$, $t_{(12)}=3.54$, $p<0.05$) but not with a mask ($M=0.90$, $t_{(12)}=2.38$, $p=0.08$). Performance with a mask did not differ significantly from that with a window ($t_{(12)}=1.16$, $p=0.50$). The main effect in response times was also significant, ($F_{(2,\ 12)}=4.30$, $p<0.05$). Again, participants were only significantly slower with a window ($M=2.34$ s) than in full view ($M=1.27$ s, $t_{(12)}=2.93$, $p<0.05$). The difference between response times in full view and with a mask was not significant ($M=1.56$ s, $t_{(12)}=2.29$, $p=0.29$); additionally, response times with a mask did not differ significantly from those with a window ($t_{(12)}=1.34$, $p=0.40$).

A bootstrap procedure with 1000 repetitions showed that, compared to full view ($M=0.96$; 95% CI=[0.91; 1.00]), the accuracy of LR was equally affected by the window ($M=0.87$; 95% CI=[0.79; 0.93]) and the mask ($M=0.88$; 95% CI=[0.80; 0.95]) (Fig. 10A). For RTs, an ANOVA on the correct response trials revealed a main effect of the viewing condition for LR (LR: $F_{(2,\ 179)}=57.40$, $p<0.0001$). Contrary to the control participants, LR was faster in full view than with a mask (LR: $t_{(179)}=10.70$, $p<0.0001$) or with a window (LR: $t_{(179)}=5.44$, $p<0.0001$) (Fig. 10B). Importantly, LR was also faster with a window than with a mask ($t_{(179)}=5.18$, $p<0.0001$), contrary to normal controls.

Crawford and Howell's (Crawford & Howell, 1998) method for the analysis of single case neuropsychological data was used to compare LR's performance directly to that of the control participants. LR's accuracy did not differ significantly from that of the age matched control participants in any of the conditions (full view: $t_{(6)}=0.47$, $p=0.33$; window: $t_{(6)}=0.15$, $p=0.44$; mask: $t_{(6)}=0.16$, $p=0.44$). His response times, on the contrary, were slower than the age matched control participants in full view ($t_{(6)}=2.017$, $p<0.05$) and with a mask ($t_{(6)}=3.55$, $p<0.01$). However, with a window, LR performed within the normal range ($t_{(6)}=0.80$, $p=0.23$) (Fig. 10).

Finally, in order to assess the differential effect of the window and mask on control participants vs. LR, we calculated the index of the RT increase due to window and mask (Fig. 11) as the difference between the performance in full view and each experimental condition, divided by the sum of these performances. LR was significantly more slowed down by the mask than the control participants ($t_{(6)}=3.867$, $p<0.01$), while the effect of the window did not significantly differ for LR and for the control participants ($t_{(6)}=0.090$, $p=0.47$).

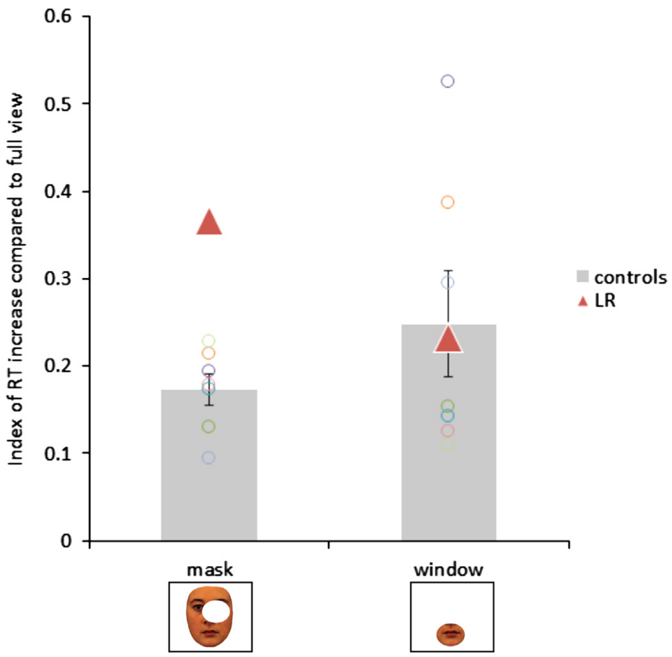

Fig. 11. Experiment 7: Gaze-contingent individual face discrimination. Index of RT increase due to window or mask compared to full view ((RTcond − RTfull)/(RTcond + RTfull). Error bars indicate standard errors.

In summary, LR is undoubtedly less severely impaired than the two cases of acquired prosopagnosia previously tested in this experiment (PS: Van Belle et al., 2010a; GG: Van Belle et al., 2011), showing accuracy rates in the normal range. However, the difficulty of the discrimination task was adjusted initially for the patient PS, in order to obtain a reasonably high performance in the full view face condition. Here, the most interesting pattern is observed in response times only, for which LR's results are completely in line with the observations made on these two cases, and opposite to normal observers: for LR, the mask condition appears to be the most difficult viewing conditions. Hence, compared to normal observers, LR's performance is affected the most when he is prevented from using a part-based process; when forced to use a part-based process, on the contrary, his performance does not differ from that of normal observers. These results support the view that, like PS and GG, LR is impaired at holistic perception of the individual face.

4. General discussion

Several experiments performed on the patient LR show that face *perception* can be specifically impaired in prosopagnosia following brain damage to the right anterior temporal lobe, sparing posterior regions. The nature of LR's impairment appears to concern holistic perception of individual faces, as is observed in cases of prosopagnosia with posterior brain damage. These results extend previous observations obtained using the same tests with two other cases of acquired prosopagnosia, PS and GG. Notably, in these two patients, brain damage concerned posterior brain areas, namely the right inferior occipital cortex and left middle fusiform gyrus for PS and the right lingual, fusiform and parahippocampic gyrus for GG, sparing the anterior temporal lobe region (see in particular Rossion et al., 2003; Ramon et al., 2010; Sorger, Goebel, Schiltz, & Rossion, 2007 for PS; Busigny et al., 2010a; Van Belle et al., 2011 for GG). Compared to these patients, the patient LR is less severely impaired in the same face discrimination tasks, whose parameters were adjusted initially for studying the patient PS. Moreover, contrary to these cases, LR's ability to process individual faces holistically may not be completely abolished, as indicated by a significant part-whole advantage in one version of the experiment 5 and a significant – albeit weaker than in controls – composite face effect in experiment 6. Nevertheless, considered altogether, these observations support the view that the nature of the critical functional impairment does not fundamentally differ across patients with acquired prosopagnosia, regardless of the localization of brain damage (Busigny et al., 2010a): all these patients appear to be impaired at what constitutes the heart of our visual expertise with faces, namely holistic perception at a sufficiently fine-grained level of resolution to discriminate exemplars of the face class efficiently (for a direct comparison of LR, PS and GG, see Busigny & Rossion, 2010b, and Supplementary material). Such a conclusion challenges the view that there are several subtypes of prosopagnosia (Damasio, Tranel, & Damasio, 1990; Schweich & Bruyer, 1993) casting doubts in particular on the dichotomy between apperceptive and associative forms of prosopagnosia (e.g., De Renzi, 1986; De Renzi et al., 1991; Barton, 2003).

4.1. Face-specificity

Experiments 1 and 2 show that LR, who never complained of any object recognition problems in real life, is able to identify objects rapidly when tested, and is not impaired at fine-grained discrimination of non-face exemplars. In a delayed matching task, he was able to match individual exemplars of various nonface categories (birds, cars, chairs, houses) as well as controls. Furthermore, his pattern of performance (i.e., slope) in a parametric individual car discrimination task mimicked normal observers' performance. However, LR was impaired at discriminating individual exemplars of faces in the exact same paradigm, despite the fact that, if anything, individual face discrimination was easier for faces than nonface objects for normal observers.[2] This pattern of performance is very similar to what was found for the patients PS (Busigny et al., 2010b) and GG (Busigny et al., 2010a), ruling out the visual similarity account of prosopagnosia (Faust, 1955; Damasio et al., 1982; Gauthier et al., 1999), and indicating that brain damage to vastly different brain structures can lead to a pure form of prosopagnosia (see also other cases, as listed in Table 1 in Busigny et al., 2010b).

[2] In a recent study, Bukach et al. (2012) claimed that LR was impaired at learning exemplars of novel objects ("Greebles"). However, there is currently no evidence that learning these stimuli requires holistic processing at individuating members of this category (Robbins & McKone, 2007; Rossion, 2013).

4.2. Impairment in holistic face perception

Although LR's impairment in holistic face perception is not as clear-cut as the patients PS and GG, our experiments 3 to 7 show that LR is impaired at holistic perception of individual faces. Indeed, the patient does not discriminate upright faces better than inverted faces, and he does not present with a typical whole-part face advantage. Interestingly, we replicated the finding that his processing of the top half of a face is influenced by the bottom half, an observation which prompted Bukach et al. (2006) to claim that LR processed faces holistically. However, this effect was qualified here by a substantial influence observed also for misaligned faces – which were not included in this previous study – specifically for LR. Most importantly, LR's pattern of performance in the gaze-contingency experiment with selective revealing/masking of a portion of the face stimulus replicates previous observations on PS and GG (Van Belle et al., 2010a; Van Belle et al. 2011, respectively) and demonstrates LR's difficulties in holistic perception of individual faces relative to normal observers.

Although Bukach et al. (2006) concluded that LR has preserved holistic processing, a careful look at the patient's data in these author's other experiments rather support the opposite view. For instance, when required to divide his attention over multiple face features, LR was able to determine the identity of only a single feature. Moreover, in a face matching task (Experiment 3, Bukach et al., 2006), LR was impaired at processing relative distances at the level of the eyes of a face, and he did not have an inversion effect in that condition. These results were replicated in a later study where LR exhibited an impaired ability to discriminate diagnostic cues in the eye region (Bukach et al., 2008). Similar observations of a severe impairment at extracting diagnostic information from the eyes have been made for the patients PS and GG (Caldara et al., 2005; Orban de Xivry, Ramon, Lefèvre, & Rossion, 2008; Rossion, Kaiser, Bub, & Tanaka, 2009; Busigny et al., 2010a) reinforcing the parallel made between the functional impairment of these patients and LR's impairment in holistic face perception. According to this view, the eye region loses its diagnosticity in acquired prosopagnosia because rapidly extracting diagnostic information from the eye region of a face requires simultaneous integration of information from multiple sources (pupils, iris, eyelids, eyebrows, distance between eyes, distance between eyes and forehead, etc.) (Caldara et al., 2005; Orban de Xivry et al., 2008; Rossion et al., 2009).

In the large majority of tests of holistic face perception, LR showed an atypical pattern of performance, and this pattern of performance was qualitatively similar to previous patients with pure prosopagnosia following brain damage tested with the same experiments (i.e., PS and GG). However, contrary to these patients, LR showed evidence for holistic face perception effects in an unusual version of the Whole-to-Part Effect (superior performance for matching parts to parts than parts to wholes). Moreover, even though LR showed an abnormal performance for misaligned trials in the composite face paradigm, his composite face effect was still significant. These observations raise the question of whether LR would be affected at a finer-grained level of holistic perception than these other patients with prosopagnosia. Indeed, holistic perception is useful not only to individualize faces, but also to detect faces, for instance when the parts of the stimulus are not face-like, as in Mooney faces (Mooney, 1957; Moore & Cavanagh, 1998; McKone, 2004) or Arcimboldo paintings (Hulten, 1987). However, face detection abilities in these three patients, as tested with Mooney and Arcimboldo face stimuli, are well preserved (See Rossion, Dricot, Goebel, & Busigny, 2011 for PS; Busigny et al., 2010a for GG; supplemental material for LR's data compared to these two patients' data). These observations indicate that all three patients are able to perceive faces holistically at a coarse level – sufficient to categorize a stimulus as a face – but not at the finest grained level (i.e. to individualize a face). However, in the absence of comparative data for other face categorizations (e.g., gender, expression, age, etc.) requiring intermediary levels of holistic representation, we cannot exclude that the patients differ in terms of the level at which they can process a face holistically. Specifically, LR may differ from patients with more posterior brain damage such as PS and GG in being able to reach a finer-grained level of holistic representation than these patients. Whether such observations would be taken as quantitative or qualitative differences between the functional impairments of the patients would certainly be a matter of debate, but at this stage the available evidence as provided here and in our previous studies point only to quantitative differences between these patients with acquired prosopagnosia.

4.3. Revisiting the concept of associative prosopagnosia

The term "holistic" has been used by many authors for face processing, and it may have different meanings in the literature (e.g., Farah et al., 1998; Maurer et al., 2002; McKone, Martini, & Nakayama, 2003; Rossion, 2008, 2009, 2013; Tanaka & Farah, 1993). However, it refers undoubtedly to a *perceptual* process, that is, the (presumably simultaneous) perceptual integration of the multiple parts of a face into a single representation. The most compelling evidence that this is a perceptual process is that it can be illustrated as a visual illusion, for instance in the well-known composite face illusion (Young et al., 1987; Rossion & Boremanse, 2008, Rossion, 2013). Hence, if LR is impaired at holistic processing of faces, this means somehow that he is unable to derive a proper percept of an individual face. His impaired performance at individual face discrimination tasks supports this claim, although most of the tasks involved a minimal short-term memory component (delayed matching in experiments 1, 2, 4, 5). LR's impaired performance at the Benton Face Recognition Test, in which he had to match simultaneously presented pictures of unfamiliar faces, further supports the view that he is impaired at *perceiving* individual faces.

The observation of a perceptual face impairment in a patient like LR, whose ventral occipito-temporal cortex up to the anterior fusiform gyrus appears entirely preserved form brain damage, challenges the very existence of pure associative forms of prosopagnosia, which has been postulated by several authors (Meadows, 1974; Benton, 1980; Damasio et al., 1982, 1990; De Renzi, 1986; De Renzi et al., 1991; Barton, 2003). Typically, the criterion for associative prosopagnosia is precisely that the patient performs normally at unfamiliar face matching tasks, such as in the Benton Face Recognition Test (Benton & Van Allen, 1968). For instance, De Renzi (1986) and De Renzi et al. (1991) claimed that their brain-damaged patients represented pure forms of associative prosopagnosia, because they were able to achieve normal range performance at this test. However, the evidence collected in these studies was often limited to a single test, with few items, no control data, and without any measure of response times. For instance, the patient 4 of De Renzi (1986) presented a score of 21/27 at the short form of the BFRT,[3] a score that was judged as high enough to exclude an impairment of perceptual nature.

Most importantly, there is substantial evidence that even prosopagnosic patients with clear perceptual impairments can use idiosyncratic strategies to compensate for their problems in unfamiliar face matching tasks and are able to reach normal levels of performance on accuracy scores at these tasks (e.g., Davidoff et al., 1986; Davidoff & Landis, 1990; Farah, 1990/2004; McNeil & Warrington, 1991; Sergent & Signoret, 1992a, 1992b; Delvenne et al., 2004). In these situations, measuring correct RTs, for instance at BFRT, systematically reveals that the patients are much slower than all normal controls. This was also the case for LR in the present study, who sometimes showed a normal performance at unfamiliar face matching tasks when considering accuracy rates only (experiments 1, 6 and 7), but who was considerably slowed down at these tasks relative to controls. Importantly, this slowing down was not found for other categories of objects (experiments 1, 2 and 4). Moreover, across all experiments, LR' slowing down relative to controls was not observed in the most difficult conditions for the controls (inverted faces, similar faces, faces revealed through a window only) or even in the conditions that were the most difficult for him in absolute terms (e.g., morphed faces that were very similar). In all these experiments, the trials of the different conditions were presented randomly. These observations exclude an explanation in terms of a general slowing down of the patient or a lack of confidence. Rather, they show that so-called cases of associative prosopagnosia can reach normal performance at a single matching test of unfamiliar faces by abnormal means, and that a perceptual impairment cannot be excluded without performing several tests and taking complementary RT measures. This is particularly the case for measurements of holistic face perception, because these effects are often revealed in response times rather than accuracy rates in normal observers (e.g., Young et al., 1987; see Rossion, 2013).

Besides the lack of stringent testing, there are other reasons why there is so little evidence of perceptual impairment in prosopagnosic patients with right anterior temporal lobe damage. First, cases of prosopagnosia with anterior temporal lesions are much less frequent than cases with more posterior lesions. Among about 120 prosopagnosic patients reported in the literature, we found only 11 patients with a lesion in the right anterior temporal lobe, while the vast majority of the patients show lesions in the right fusiform gyrus and in the right inferior occipital gyrus (see also Bouvier & Engel, 2006). One reason for that is that the principal etiology of prosopagnosia is an ischemic stroke, specifically in the territory of the right posterior cerebral artery. By contrast, lesions of the right anterior temporal lobe are principally reported in the context of a degenerative disorder, i.e., the right temporal lobe variant of frontotemporal dementia (e.g., Joubert et al., 2006; Gainotti, 2007). Most of the time, these patients have multimodal and multicategorical impairment, preventing them to recognize faces, but also other categories (e.g., famous places), and via different modalities (pictures, names, voices,…) (see Gainotti, 2007, 2013; Busigny et al., 2009). In these cases, the nature of the defect is generally semantic, and the patients cannot be considered strictly as prosopagnosic, since they do not present with a recognition defect limited to the visual modality (see Gainotti, 2013). Thus, prosopagnosic patients after a lesion of the anterior temporal lobe are rare, most patients with this kind of damage having multimodal person recognition defects. Given that he has visual impairment in face recognition, but does not have any difficulties in recognizing people from their names and providing semantic information about them, LR is one of these rare patients.

Nevertheless, these observations on LR are in line with the description of two cases of prosopagnosia, TS (Barton et al., 2003) and BD (Williams, Savage, & Halmagyl, 2006), who had damage restricted to the right anterior temporal lobe and were impaired at perceiving faces. Interestingly, both of these patients were

[3] While such a performance could presumably be equated to a score of 42/54 at the long form of the test, slightly above a score within the norms, it should be qualified because the patients are usually faultless at the first 6 items of this test, all included in the short form, where only one target face has to be found among 6, without any change of viewing conditions. If these items are excluded, De Renzi (1986)'s patient had a score of 15/21 (70%) at a single unfamiliar face matching task, a performance that is insufficient to exclude a perceptual impairment with faces.

probably impaired at holistic face processing, TS being insensitive to the global spatial configuration that differs between faces, and BD having a disrupted composite face effect. Furthermore, a study of anterior temporal lobectomized patients showed a correlation between these patients' face naming impairment and their perceptual discrimination of unfamiliar faces (Glosser et al., 2003). Together with our results, these observations support the claim that anterior temporal lobe structures of the right hemishere play a role in binding together information relevant to the perceptual identification of unique entities such as individual faces.

To summarize this point, we argue that the apperceptive/associative distinction used to refer to cases of prosopagnosia is misleading and should perhaps be abandoned. We hypothesize that when tested stringently, other cases of prosopagnosia following focal brain damage, even those with damage restricted to the (right) temporal pole, may be impaired at face perception. As mentioned in the introduction, these observations are in line with the claim of Farah (1990/2004), that "*perception is at fault in all cases of associative agnosia so far studied*" (Farah, 1990/2004, p. 75). In fact, Lissauer himself qualified his own distinction between apperceptive and associative visual agnosia because he noted that the full perception of complex visual stimuli such as facial figures requires an appropriate linkage with stored representations (Lissauer, 1890; Shallice & Jackson, 1988). Hence, according to this latter view, the cause of prosopagnosia cannot be strictly divided into a perceptual vs. a mnesic impairment. The case study of LR illustrates the difficulty of building a proper perceptual representation of an individual face following damage to neural structures that are important in linking perceptual and associative representations.

4.4. The right anterior temporal lobe: a critical node in a face perception network

Although we must remain careful in the absence of detailed anatomical and functional data (i.e., (f)MRI)) of the patient LR, our observations in this patient and the description of other such cases as mentioned above point to a role of the right anterior temporal lobe in face perception, and specifically in holistic perception of individual faces.

Face perception is supported by an extensive neural network that encompasses regions of the ventral occipito-temporal pathway, with a right hemispheric dominance (Sergent et al., 1992; Haxby et al., 2000; Fox et al., 2009; Weiner & Grill-Spector, 2010; Davies-Thompson & Andrews, 2012; Rossion et al., 2012; Pyles et al., 2013). This network involves, at least, a face-selective functional region in the lateral middle fusiform gyrus (called the "Fusiform Face Area", "FFA", Kanwisher, McDermott, & Chun, 1997; McCarthy, Puce, Gore, & Allison, 1997), another in the lateral inferior occipital cortex ("Occipital Face Area", "OFA", Gauthier et al., 2000; Rossion et al., 2003) and yet another one in the posterior part of the superior temporal sulcus (Puce, Allison, Bentin, Gore, & McCarthy, 1998; Allison, Puce, & McCarthy, 2000; Hoffman & Haxby, 2000), all three regions being dominant in the right hemisphere. These regions have been described as the core face-perceptual network (Haxby et al., 2000), with the FFA and OFA at least showing clear sensitivity to individual faces discrimination (e.g., Gauthier et al., 2000; Grill-Spector & Malach, 2001; Schiltz & Rossion, 2006; Andrews, Davies-Thompson, Kingstone, & Young, 2010).

In this context, what would be the role of the right anterior temporal lobe in face perception? One possibility is that this region also plays a direct role in individual face perception, but that the strong emphasis on the FFA (and to a lesser extent the OFA), coupled with the presence of strong magnetic susceptibility artifacts in the anterior temporal lobe (ATL, Devlin et al., 2000; Bellgowan, Bandettini, van Gelderen, Martin, & Bodurka, 2006), has hidden its contributing role. Nevertheless, face-specific activation has been reported in the human anterior temporal lobe, particularly in the right hemisphere (e.g., Rajimehr, Young, & Tootell, 2009; Rossion et al., 2012). Moreover, recent neuroimaging studies suggested that the right anterior temporal lobe is also involved in individual face discrimination, even when the stimuli are not explicitly associated with any biographical or semantic information (Kriegeskorte, Formisano, Sorger, & Goebel, 2007; Furl, van Rijsbergen, Treves, & Dolan, 2007; Pinsk et al., 2009).

However, the right ATL has also been described as having a crucial function in face memory and semantic knowledge about people (e.g., Gorno-Tempini & Price, 2001; Snowden, Thompson, & Neary, 2004; Thompson et al., 2004; Rogers et al., 2006; Olson, Plotzker, & Ezzyat, 2007; Drane et al., 2008; Tsukiura, Suzuki, Shigemune, & Mochizuki-Kawai, 2008; Simmons, Reddish, Bellgowan, & Martin, 2010). Hence, along the lines of Lissauer (1890)'s insightful view, one may also consider that this region plays a role in the storage, consolidation and linking of perceptual representations, and that such dynamic associations are necessary to achieve a fully refined perceptual representation of an individual face. That is, rather than seeing the perceptual impairment as being causal, one would see it the other way around: damage to areas primarily involved in associative memory could cause a defect in face perception. These observations are in line with the Emergent Memory Account (EMA; Barense, Gaffan, & Graham, 2007; Graham, Barense, & Lee, 2010), which suggests that perception and memory depend on an overlapping network of widespread representations, and that memory is the outcome of a dynamic interplay between hierarchically organized perceptual representations distributed throughout the brain. This complex entanglement between perception and memory implies that the way we perceive visually is influenced by our stored representations. In other words, complex (multidimensional) percepts emerge from the automatic associations of simple, non category-specific representations, through the matching with internal holistic representations. Considering this, in the case of LR for instance, a lesion in the anterior temporal lobe appears to have negative effects on perceptual processing of faces, suggesting that the right anterior temporal cortex plays a crucial role in the interplay between memory and perception of faces.

5. Conclusions

In conclusion, we report a case of prosopagnosia following right anterior temporal damage who is specifically impaired with the holistic perception of individual faces. Taken together with results obtained from other cases of acquired prosopagnosia, these observations suggest that complex (multidimensional) face percepts emerge from the automatic associations of simple, non category-specific representations, through the matching with internal face representations. A crucial process involved at that level is the holistic/configural perception of individual faces. An individual face can be fully perceived as a single entity only if it can be successfully associated with an internal holistic face representation. This process may be successfully completed only if a whole network of posterior and anterior cerebral regions is functionally intact. In this framework, the notion of pure associative prosopagnosia, namely, a patient impaired at face recognition who would be able to derive a correct percept of a face, should be reconsidered. At the functional level, although the degree of severity of the face recognition impairment and the kind of associated deficits can greatly vary among patients, our findings raise the possibility that there is a single form of acquired prosopagnosia.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.neuropsychologia.2014.01.018.

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