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Holistic perception of the individual face is specific and necessary: Evidence from an extensive case study of acquired prosopagnosia

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ABSTRACT

We present an extensive investigation (24 experiments) of a new case of prosopagnosia following right unilateral damage, GG, with the aim of addressing two classical issues: (1) Can a visual recognition impairment truly be specific to faces? (2) What is the nature of acquired prosopagnosia? We show that GG recognizes nonface objects perfectly and quickly, even when it requires fine-grained analysis to individualize these objects. He is also capable of perceiving objects and faces as integrated wholes, as indicated by normal Navon effect, 3D-figures perception and perception of Mooney and Arcimboldo face stimuli. However, the patient could not perceive individual faces holistically, showing no inversion, composite, or whole-part advantage effects for faces. We conclude that an occipito-temporal right hemisphere lesion may lead to a specific impairment of holistic perception of individual items, a function that appears critical for normal face recognition but not for object recognition.

1. Introduction

The ability to recognize people from their face is a fundamental brain function which holds a high social value. It is also an extremely complex function, which is nevertheless performed quite well in human adults. The adult human brain has developed mechanisms allowing, for instance, recognizing a familiar person from its face in less than half a second (Bruce & Young, 1986), or encoding new faces in memory effortlessly during the entire life (e.g., Bahrick, Bahrick, & Wittinger, 1975). Yet, interestingly, the field of face recognition was originally based upon the study of people who, following brain damage, have lost this expertise in recognizing faces.

Difficulty in face recognition as a major symptom in patients with cerebral disease was first reported in the nineteenth century (Charcot, 1883; Quaglino & Borelli, 1867; Wigan, 1844; Wilbrandt, 1887). However, it was Bodamer (1947) who proposed to isolate the disorder on the basis of three cases, and introduced the term *prosopagnosia* from the Greek "*prosopon*" (face) and "*a-gnosia*" (without knowledge). Prosopagnosia is classically defined as the inability to recognize individual faces following brain damage, an impairment that cannot be attributed to intellectual deficiencies or low-level visual problems (Benton, 1980; Bodamer, 1947; Hécaen & Angelergues, 1962; Rondot & Tzavaras, 1969). Prosopagnosic patients also generally still retain their ability to recognize people by other cues: the voice or other visual traits such as gait, size, clothes, or even facial features (moustache, scar, freckles, ...) or accessories (ear-rings, eyeglasses, piercings, ...).

Over the years, tens of cases of prosopagnosia following brain damage have been reported, although extensive neuropsychological investigations of prosopagnosic patients remain quite rare (e.g., Anaki, Kaufman, Freedman, & Moscovitch, 2007; Barton, 2008a; Delvenne, Seron, Coyette, & Rossion, 2004; Lhermitte, Chain, Escourolle, Ducarne, & Pillon, 1972; Riddoch, Johnston, Bracewell, Boutsen, & Humphreys, 2008; Rossion et al., 2003; Sergent & Signoret, 1992a; Sergent & Villemure, 1989).

Both in traditional (cognitive) neuropsychology and in modern cognitive neuroscience, the lesion method is seen as an invaluable and unique way of understanding normal brain function (e.g., Caramazza, 1986; Damasio & Damasio, 1989; Farah, 1990; Farah, 2004; Humphreys & Riddoch, 1987; Shallice, 1988), in particular with respect to face recognition. Such patient studies contribute to shaping our knowledge and conceptions of the processes involved in normal face recognition and their underlying neural networks.

From a functional point of view, there are two main debates concerning prosopagnosia, which have direct implications for understanding face recognition: (1) Can the impairment truly be restricted to face recognition (i.e. *face-specific*)? (2) What is the

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nature of the disorder, that is, what is at the heart of our expertise in facial recognition, and which is lost in these patients? These two issues have proved quite difficult to resolve and are still debated (e.g., Barton, 2009; Damasio, Damasio, & Van Hoesen, 1982; De Renzi, 1986a; Hécaen, 1981; Riddoch et al., 2008; Rondot & Tzavaras, 1969; Sergent & Signoret, 1992a).

1.1. Prosopagnosia as a face-specific disorder

The issue of the specificity of the disorder has been complicated by the fact that most reported cases of prosopagnosia also present with difficulties in basic-level object recognition (e.g., Barton, 2008a; Boutsen & Humphreys, 2002; Damasio et al., 1982; Delvenne et al., 2004; Gauthier, Behrmann, & Tarr, 1999; Levine & Calvanio, 1989; Steeves et al., 2006). In many other cases, object recognition abilities were not tested sufficiently (e.g., De Renzi, 1986a; Ettlin et al., 1992; Tohgi et al., 1994; Young, Flude, Hay, & Ellis, 1993). A brief but extensive review of the neuropsychological literature points to 13 prosopagnosic patients who could be considered as presenting with a face-specific recognition disorder (Table 1). De Renzi (1986a) presented patient 4 who performed in the normal range at object and figure recognition, figure–ground discrimination, visual closure and segmentation. Patient VA (De Renzi, Faglioni, Grossi, & Nichelli, 1991) could name objects and pictures (presented under usual and unusual view) in the normal range, and succeeded at tasks of visual closure, coin discrimination, and recognition of makes of cars and personal belongings. Another patient described by De Renzi, Perani, Carlesimo, Silveri, and Fazio (1994), OR, was documented to present with an absence of impairment with respect to object naming, Italian coins discrimination, and recognition of animals, fruits and vegetables (under usual and unusual views). Takahashi, Kawamura, Hirayama, Shiota, and Isono (1995), in a study of four patients, related the case of a patient with apparently no object recognition impairment: case 3 succeeded in different tasks including overlapping figures, Gestalt completion test, Kanizsa triangle and real object naming. Schweinberger, Klos, and Sommer (1995) and Henke, Schweinberger, Grigo, Klos, and Sommer (1998) showed that the performance of patient MT was preserved in numerous tasks: recognizing overlapping figures, Gestalt completion task, object naming, animal naming and different series of similar objects to name (fruits and vegetables, symbols of German industrial brands and cars brands). Patient WB (Buxbaum, Glosser, & Coslett, 1996) presented with preserved object naming (real objects and drawings) and memory for homogeneous category of objects (glasses, under different views). Patient Anna (De Renzi & di Pellegrino, 1998) succeeded in several tasks: objects naming (color photographs and line drawings), perceptual categorization, visual segmentation and closure, and memory for homogeneous category of objects (glasses, under different views). Another study (Wada & Yamamoto, 2001) also reported a prosopagnosic patient who could perform well the tasks of overlapping figures, picture copying, recognition of letters and symbols, visual space perception, object naming (real objects, pictures, line drawings; under usual and unusual view), animal face and famous place recognition. Prosopagnosic patient PS was able to recognize objects perfectly and rapidly (Rossion et al., 2003) and could perform within-category discrimination for nonface items in the normal range of performance and speed (Busigny, Graf, Mayer, & Rossion, 2010; Schiltz et al., 2006). Barton and colleagues reported case 009 (Barton, 2008a, 2009; Barton & Cherkasova, 2005; Barton, Cherkasova, Press, Intriligator, & O'Connor, 2004), a patient who had no low-level visual impairment and was able to recognize incomplete letters, overlapping figures, real objects, vegetables and fruits, presented with a classical Navon effect, and showed some ability to process configurations of dots. Bukach, Bud, Gauthier, and Tarr, 2006 and Bukach, Le Grand, Kaiser, Bub, and Tanaka, 2008 related another case of selective impairment for faces, LR, who succeeded easily in tasks of low-level visual processing, silhouettes and object naming (under usual and unusual views). Riddoch et al. (2008) presented the case of FB, who had preserved abilities in low-level visual processing, non-living and living (birds, flowers, vegetables and fruits) objects naming, and in a task of learning associations between names and novel multipart objects. Finally, Rivest, Moscovitch, and Black (2009) published the case of DC, who performed normally in segmented object recognition, object naming, recognition of famous buildings and dog breeds.

These pure cases of acquired prosopagnosia suggest that some processes may be *necessary* to recognize faces efficiently, and that these processes may be selectively disrupted by brain damage. While these processes might also be involved in object recognition, they would not be necessary for this function.

1.2. The holistic perception account of prosopagnosia

Regarding the *nature* of the impairment in prosopagnosia, an influential idea is that such patients have difficulties in *perceiving a face as a whole, or a Gestalt*. This long-standing view (Galli, 1964) is inspired originally from the Gestaltist approach of visual perception (e.g., Koffka, 1935/1963; Kohler, 1929; 1930/1971; Wertheimer, 1925/1967). According to the Gestaltist view and its more modern revival (e.g., Kubovy & Poremantz, 1981; Navon, 1977; for a review see Kimchi, 1992), a whole item is qualitatively different from the sum of the components, the whole exceeding the sum of its parts. Hence, what takes place in each single part already depends upon what the whole is: objects are not only made of featural elements, but also defined by the interactions between these constituents, a property that is called *configuration* or *(w)holistic property* (e.g., Navon, 2003). For instance, a face is a typical visual stimulus made of parts (eyes, nose, mouth, . . .) that are organized in a whole configuration (a symmetrical structure with two eyes on top, above a central nose and mouth).

The idea that acquired prosopagnosic patients lose their ability to perceive faces holistically is supported at four levels.

First, many patients have been described as presenting with a configural/holistic[1] processing impairment, that is, an inability to integrate simultaneously different features into a coherent global representation (RB, Davidoff, Matthews, & Newcombe, 1986; HJA, Boutsen & Humphreys, 2002; Riddoch & Humphreys, 1987; LH, Levine & Calvanio, 1989; BM, Sergent & Villemure, 1989; WL, Spillmann, Laskowski, Lange, Kasper, & Schmidt, 2000; AR, Saumier, Arguin, & Lassonde, 2001; RC, Wilkinson et al., 2009; PS, Ramon, Busigny, & Rossion, 2010). For example, Levine and Calvanio (1989) described the patient LH as being unable to "*get an immediate overview of a face [. . .] as a whole at a single glance*" (p. 159). They conceptualized this loss of visual "*configural [i.e. holistic] processing*" as a deficit in visual perception reflected by the inability to derive an "*overview of sufficient features to allow structuring or crystallization of a coherent concept*". In the same vein, Spillmann et al. (2000) described the prosopagnosic patient WL as following: "*he was unable to form a holistic percept of a given face that would have revealed its bearer's identity. Rather, he used conspicuous features for recognition [. . .]. Recognition was based on characteristic details, not faces per se [. . .]. What seems to be lacking in WL is the ability to create an integrated, unitary percept or a gestalt of a human face enabling him to assign identity to an individual*" (pp. 93, 98).

[1] In this paper, in keeping with earlier studies in the field of face recognition and recent reviews of this issue, the terms holistic and configural are used interchangeably, as synonyms, to refer to the same process (see McKone & Yovel, 2009; Rossion, 2008a; Rossion, 2009).

Second, very few cases of acquired prosopagnosia with preserved holistic face processing have been reported (PV, Sergent & Poncet; PC, Sergent & Signoret, 1992a; LR, Bukach et al., 2006). Moreover, holistic processing was not tested extensively and with particularly sensitive tests in these patients, so that it remains unclear to what extent their holistic processing of faces was truly preserved (see Ramon et al., 2010). This issue will be addressed more extensively in Section 4.

Third, there is to date no solid and more accurate alternative hypothesis to account for the functional impairment characterizing acquired prosopagnosia. For instance, the few alternative proposals in terms of low-level processing are no longer valid. Indeed, an account of prosopagnosia – or visual agnosia – in terms of sensory or low-level visual impairments (Bay, 1953; Ettlinger, 1956), has been dismissed for some time (De Haan, Heywood, Young, Edelstyn, & Newcombe, 1995; Rondot & Tzavaras, 1969), and many prosopagnosic patients do not suffer from low-level visual problems (e.g., Bukach et al., 2006; Buxbaum et al., 1996; Delvenne et al., 2004; Dixon, Bub, & Arguin, 1998; Eimer & McCarthy, 1999; Schweinberger et al., 1995; Sergent & Poncet, 1990; Wada & Yamamoto, 2001). Even when low-level vision is impaired, such as color vision (i.e. achromatopsia, as in many cases of prosopagnosia, see Bouvier & Engel, 2006), or visual defects in the left upper quadrant (Bouvier & Engel, 2006; Hécaen & Angelergues, 1962; Meadows, 1974) these associated defects cannot account for the face recognition impairment (Rondot & Tzavaras, 1969).

Fourth and finally, alternative views of prosopagnosia which consider this syndrome as a high-level visual defect can be easily integrated into a holistic processing impairment account. For instance, it has been suggested that the processing of the region of the eyes in faces is particularly problematic for prosopagnosic patients (Gloning, Gloning, Hoff, & Tschabitscher, 1966), a proposal which has received recent empirical support by studies showing a reduced diagnosticity of the region of the eyes of faces for the patients PS (Caldara et al., 2005; Rossion, Kaiser, Bub, & Tanaka, 2009) and LR (Bukach et al., 2006, 2008). However, the reason why these patients do not rely on the eyes region, and fixate this region less often than normal observers during face recognition (Orban de Xivry, Ramon, Lefèvre, & Rossion, 2008), may be directly related to their inability to process individual faces holistically. Indeed, for a patient who cannot encode the individual features of the face as a single representation, it may be better to focus on an isolated feature (e.g., the mouth) which may contain in itself more information than each of the elements of the eye region considered in isolation (see Caldara et al., 2005; Orban de Xivry et al., 2008; Rossion et al., 2009; Van Belle, de Graef, Verfaillie, Busigny, & Rossion, 2010). In the same vein, an impairment in perceiving relative distances between features in prosopagnosia (Barton, 2009; Barton & Cherkasova, 2005; Barton, Press, Keenan, & O'Connor, 2002) may be a *consequence* of the difficulty to perceive the face as a whole (Ramon & Rossion, 2010; Rossion, 2008a; Rossion, 2009; Sekunova & Barton, 2008). These issues will be developed further in the present paper.

1.3. Holistic perception and pure prosopagnosia: a paradox and a proposal

Given these considerations, the holistic perception account of (acquired) prosopagnosia can be considered to be the dominant view. However, there is at least one important issue that needs to be resolved: since object recognition is based – at least to some extent – on the ability to perceive an object or a general visual pattern holistically (e.g., Kimchi, 1992; Kimchi, 2000; Navon, 1977), how could prosopagnosia be specific to faces if what characterizes prosopagnosic patients is an impairment in holistic perception? This paradox is reinforced by the fact that most case studies who support the holistic account of prosopagnosia have reported patients who suffer from important object recognition impairments, and who were actually tested with non-face objects (e.g., HJA, Riddoch & Humphreys, 1987; LH, Levine & Calvanio, 1989; WL, Spillmann et al., 2000; AR, Saumier et al., 2001; CR, Behrmann & Williams, 2007; Gauthier et al., 1999; SM, Behrmann & Kimchi, 2003; Behrmann & Williams, 2007; Gauthier et al., 1999; RN, Behrmann & Kimchi, 2003; NS, Delvenne et al., 2004).

To resolve this issue, one may consider that nonface objects are perceived in a part-based manner (Biederman, 1987; Marr, 1982; Treisman, 1986), while faces only would be perceived holistically (Biederman & Kalocsai, 1997; Moscovitch, Winocur, & Behrmann, 1997; see also McKone, Martini, & Nakayama, 2003). However, there are numerous instances in which a nonface object pattern is perceived holistically (e.g., Kimchi, 1992; Navon, 1977).

Another way to resolve this issue is by proposing that faces are processed *more* holistically than other objects (Farah, 1990, 2004). That is, while object perception would depend on both part-based and holistic processes, faces would depend exclusively on holistic processes. Depending on severity of the impairment, patients would be either prosopagnosic only, or prosopagnosic *and* object agnosic (Farah, 1990, 2004). However, it is unclear based on this account how "the severity" of the impairment can be assessed, and thus how the recognition impairment may be completely restricted to faces in certain cases. In fact, this view was inspired by investigations carried out on the patient LH, a case of prosopagnosia who also presented with a severe impairment in object recognition (Farah, Wilson, Drain, & Tanaka, 1995; Levine & Calvanio, 1989; Levine, Calvanio, & Wolf, 1980).

Finally, since most case studies supporting the holistic account of prosopagnosia have reported patients who are impaired at nonface object recognition (Behrmann & Kimchi, 2003; Behrmann & Williams, 2007; Delvenne et al., 2004; Gauthier et al., 1999; Levine & Calvanio, 1989; Saumier et al., 2001; Spillmann et al., 2000), it may be that the few cases of pure prosopagnosia reported in the literature (Table 1) do not suffer from an impairment at holistic processing. However, while holistic object perception has been tested and found normal in some of these patients (see Table 1), their ability to process faces holistically remains largely unclear. Moreover, there is evidence collected from separate studies performed in at least one of these cases of prosopagnosia (PS) that visual recognition difficulties can be truly restricted to faces (Rossion et al., 2003; Schiltz et al., 2006), and yet concern holistic perception of faces (Busigny & Rossion, 2010; Ramon et al., 2010; Van Belle, de Graef, Verfaillie, Busigny, et al., 2010).

Here we suggest that none of the above proposals is satisfying, and that the key issue is not that face recognition would be "more" holistic than object recognition, or that objects would not be processed holistically. Rather, we suggest that both basic-level face and object categorization ("it is a face"; "it is a banana") rely on holistic processes. These processes are impaired in patients suffering from integrative visual agnosia, and these patients also suffer from prosopagnosia. When an individual item of a visual category has to be identified and/or differentiated from other individuals from the same category, normal observers would rather rely largely on part-based processes. In contrast, individualizing faces would still require the ability to perceive (the *individual* item) holistically. That is, contrary to nonface objects, fine-grained discrimination of individual faces would also depend critically on the ability to perceive faces holistically (Biederman & Kalocsai, 1997).

If this hypothesis is true, a patient with pure prosopagnosia following brain-damage, should have (1) preserved basic-level *object* recognition, even when holistic processing is required; (2) preserved *face* detection, even when holistic processing is required; (3) preserved individual level *object* recognition, that is, when fine-grained discrimination is required. However, the patient should

Table 1
A summary of the findings for the 13 "pure prosopagnosic" patients reported in the literature.

Authors	Case	Lesion	Objects	Faces
De Renzi (1986a)	Patient 4	Right parahippocampal gyrus, lingual gyrus, fusiform gyrus, calcarine fissure, cuneus	- Figure-ground discrimination: OK - Visual closure: OK - Overlapping figures: OK - Object naming: OK	- BFRT (short form): KO (18/27) - Memory of new faces: KO
De Renzi et al. (1991)	VA	Right temporal lobe	- Visual closure: OK - Object naming (usual and unusual view): OK - Coin discrimination: OK - Recognition of personal belongings: OK - Makes of cars naming: OK	- BFRT (short form): OK (21/27, no RTs) - Familiarity judgment: KO - Famous faces designation: KO
De Renzi et al. (1994)	OR	Right temporal lobe involving T3, T5 and T6; right parietal lobe involving P1 and P2	- Object naming: OK - Recognition of animals, fruits, vegetables (usual AND unusual views): OK - Italian coins discrimination: OK	- Matching of unknown faces: KO - Familiarity judgment: KO - Famous faces designation: KO
Takahashi et al. (1995)	Case 3	Right temporo-occipital lobe, involving fusiform and lingual gyri	- Visual segmentation: OK - Gestalt completion test: OK - Kanizsa triangles: OK - Real object naming: OK	- BFRT (Japanese version): OK (42/54, no RTs) - Same/different judgment: OK - Memory of new faces: KO - Familiar faces recognition: KO
Schweinberger et al. (1995) and Henke et al. (1998)	MT	Right temporo-parietal lobe, also extending in frontal and occipital areas	- Visual segmentation: OK - Visual closure: OK - Object naming (line drawings): OK - Animals naming: OK - Similar objects naming (fruits and vegetables; symbols of German industrial brands; cars brands): OK	- BFRT: KO (37/54, very slow) - Memory of new faces: KO - Famous faces recognition: KO
Buxbaum et al. (1996)	WB	Bilateral occipital lobes	- Object naming (real objects; drawings): OK - Memory for homogeneous category of objects (glasses, different views): OK	- BFRT: KO (20/54) - Memory of new faces (different views): KO - Famous faces recognition: KO
De Renzi and di Pellegrino (1998)	Anna	Bilateral posterior cingulate gyrus, infra- and supracalcarine areas, mesial part of the superior parietal lobe	- Perceptual categorization: OK - Visual segmentation: OK - Visual closure: OK - Object naming (color photographs; drawings; Snodgrass and Vanderwart): OK - Memory for homogeneous category of objects (glasses, different views): OK	- BFRT (short): OK (21/27, no RTS) - Memory of new faces (same view): OK - Memory of new faces (different views): KO - Famous faces designation: OK - Familiarity judgment: KO - Famous faces recognition: KO
Wada and Yamamoto (2001)		Right infero-occipital lobe, involving fusiform gyrus and lateral occipital region	- Low-level visual processing (line length, counting dots, shapes, line orientation): OK - Visual segmentation: OK - Recognition of letters and symbols: OK - Object naming (real objects; pictures; line drawings; usual/unusual views): OK - Famous places naming: OK - Animal face naming: OK	- Matching unfamiliar faces: KO - Memory of new faces: KO - Familiarity judgment on famous faces: KO - Famous faces recognition: KO - Familiarity judgment on familiar faces: KO - Familiar faces recognition: KO
Rossion et al. (2003), Schiltz et al. (2006) and Busigny and Rossion (2010)	PS	Right infero-occipital lobe and middle temporal gyrus; left mid-ventral gyrus and posterior cerebellum	- Low-level visual processing (BORB): OK - Object decision: OK - Object naming (colored Snodgrass and Vanderwart): OK - Between- and within category discrimination: OK - Homogeneous categories (multi-parts novel objects, cars): OK	- BFRT: KO (27/54, very slow) - WRMT: KO - Matching unfamiliar faces (same view; different views): KO - Familiarity judgment: KO - Famous faces recognition: KO - Face inversion effect: KO - Whole-part face advantage: KO - Composite face effect: KO - Eyes processing: KO
Barton et al. (2004), Barton (2008a, 2008b, 2009) and De Gelder et al. (2003)	009	Right occipito-temporal lobe, involving fusiform gyrus	- Low-level visual processing (VOSPB): OK - Incomplete letters: OK - Visual segmentation: OK - Navon effect: OK - Object decision: OK - Vegetable and fruit identification: OK - Dot-displacement discrimination (2 and 4 dots): OK	- Benton: OK (43/54, no RTs) - WRMT: KO - Familiarity judgment: KO - Whole-part face advantage: KO - Within-face spatial perception: KO - Discriminating changes in face configuration: KO

Table 1 (*Continued*)

Authors	Case	Lesion	Objects	Faces
Bukach et al. (2006)	LR	Right infero-anterior temporal lobe and amygdala	- Low-level visual processing (VOSPB, Benton line): OK - Silhouettes recognition: OK - Object naming (noncanonical view; Snodgrass and Vanderwart): OK	- Benton: acc OK (49/54) but RTs very slow and feature-by-feature strategy - Benton (17sec cutoff version): KO (12/54) - WRMT: KO - Familiarity judgment: KO - Famous faces recognition: KO - Face inversion effect: KO - Configural processing (spatial relations): KO - Eyes processing: KO
Riddoch et al. (2008)	FB	Right inferior occipital lobe, inferior and middle temporal lobe, fusiform gyrus	- Low-level visual processing (BORB, VOSPB): OK - Object naming (non-living; living: birds, flowers, vegetables, fruits): OK - Learning associations name/novel multipart object: OK	- Matching faces (different views): KO - WRMT: KO - Familiarity judgment: KO - Familiarity judgment: KO - Famous faces recognition: KO - Face inversion effect: KO
Rivest et al. (2009)	DC	Bilateral medial occipital lobe, involving lingual gyrus and cuneus; right fusiform gyrus and frontal lobe	- Low-level visual processing (VOSPB): OK - Visual segmentation: OK - Object naming (Boston naming test): OK - Recognition of famous buildings: OK - Recognition of dog breeds: OK	- Benton: KO (40/54, impaired in comparison of age-matched controls) - Matching front view faces: OK - Matching side view faces: OK - Matching side-front faces: KO - Famous faces naming: KO

BORB, Birmingham Object Recognition Battery (Riddoch & Humphreys, 1993).
VOSPB, Visual Object and Space Perception Battery (Warrington & James, 1985).
BFRT, Benton Facial Recognition Test (Benton et al., 1983).
WRMT, Warrington Recognition Memory Test (Warrington, 1984).

be impaired at individual face recognition/discrimination, and be insensitive – or significantly less sensitive than normal observers – to the classical effects measuring holistic processing of the individual face (Tanaka & Farah, 1993; Young, Hellawell, & Hay, 1987).

As mentioned above, over the last few years, we have reported evidence supporting most of these claims from investigations of the prosopagnosic patient PS in separate studies (Busigny & Rossion, 2010; Busigny & Rossion, in press; Ramon et al., 2010; Rossion et al., 2003; Schiltz et al., 2006). Here, our goal was to fully address this crucial issue in a complete and exhaustive case study of a new case of prosopagnosia.

To this aim, we report the patient GG, who suffered from a stroke in 2003 in the territory of the right posterior cerebral artery, causing focal posterior right hemisphere brain damage. No controlateral (left hemisphere) insult was evidenced on structural (MRI) and perfusion (SPECT) brain studies. This patient is particularly interesting to test our hypothesis, because, while being a very conscientious and dedicated man who was alert and cooperative throughout the study, he did not and does not complain at all of object recognition difficulties in real life. Moreover, like many acquired prosopagnosic patients, when he had to describe his face recognition difficulties he mentioned that he was no longer able to build a “global picture” of faces. Rather, in order to recognize faces, he reported trying to identify a particular feature (pimple, wart, very big green eyes, red hair, freckles, . . .). GG thus provided us with a unique opportunity to better understand the nature of the face processing impairment in prosopagnosia.

2. Methods

2.1. GG: clinical history

GG is a right-handed male and retired computer engineer born in 1942. He presented in 2002 at the Neurology and Neuropsychology unit of the Timone Hospital (Marseille, France) for a cerebral vascular accident. He sustained an ischemic infarct in the territory of the right posterior cerebral artery. Consecutively to this, GG suffered from hemianopsia and prosopagnosia. Contrasting with his previously excellent memory for faces (according to himself and his spouse), the patient complained about severe difficulties to recognize familiar faces: ex-colleagues, neighbours, shopkeepers, etc. He also had trouble recognizing many famous people on television (actors, politicians, sportsmen, etc.), his colleagues in a painting class he met on a weekly basis as well as old friends from a war veterans association. He was also no longer able to follow TV series because he was mixing up the characters and was unable to learn new faces. Because GG has no more contacts with his family, recognizing close members of his family was not an issue.

The second main complaint of GG was his inability to orient himself in space (topographical disorientation). He mentioned having difficulties finding his way in new places. As a consequence of his handicap, GG complained of a decrease in motivation and social activity, and of becoming more irritable.

GG had no prior history of neurological or vascular disease. He was well aware of his difficulties, which were all confirmed by his spouse. GG’s ophthalmologic assessment showed a left lateral homonymous hemianopsia (Fig. 1A) which, nevertheless, did not prevent him from performing a large number of tasks extremely efficiently. GG gave informed consent before testing. With the exception of a small additional experiment done in June 2010 (in experiment 5), all investigations took place between September 2003 and August 2007.

2.2. Neuroradiological findings

A structural MRI obtained in November 2003[2], approximately one year after GG’s stroke, showed clear damaged brain tissue in the occipital lobe, the fusiform gyrus, and the parahippocampal gyrus, unilaterally in the right hemisphere (Fig. 1B). MRI displayed also mild microvascular changes within the lentiform nucleus. These MRI findings were confirmed by SPECT examination. The 3D Talairach cortical perfusion report showed hypoperfusion restricted to the internal parts of the right occipito-temporal cortex (Fig. 1C).

2.3. General neuropsychological assessment

GG first underwent a general neuropsychological assessment in November 2003 and a follow-up neuropsychological evaluation in January 2007. The results are summarized in Table 2.

The results of the first standard neuropsychological assessment indicated that GG had preserved abilities in all cognitive domains: full-scale IQ, visuo-perceptual and visuo-spatial skills, praxic and executive functioning, language, reading and memory. His visual memory performance was in the lower range in the Rey-Osterreich figure recall, but his results were normal at all other visual memory tasks. The lower range results in this task probably reflect more some difficulties in spatial organization (due to the large right parahippocampal lesion) than a visual memory impairment. Otherwise, the patient was very efficient in all tasks. He succeeded very well at all the visuo-perceptual tasks, suggesting that he did not present with general visual agnosia, and was also completely in the normal range with respect to semantic tests, thereby dismissing a semantic impairment. We would like particularly to emphasize the exceptional results of GG in the naming task of Snodgrass

[2] A recent MRI (June 2010) showed the exact same extent of brain damage.

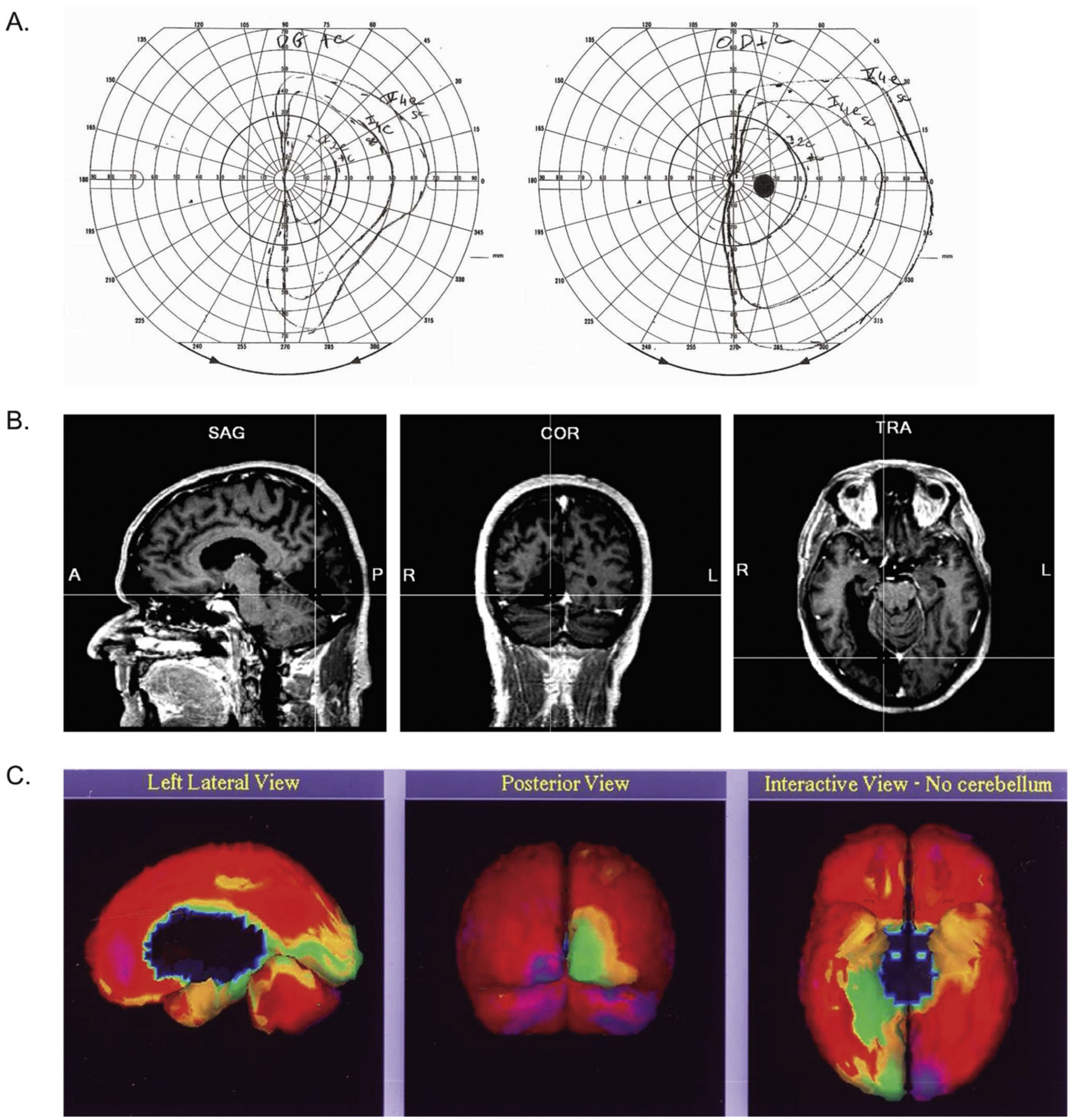

Fig. 1. (A) GG's ophthalmologic assessment showing a left lateral homonymous hemianopsia. (B) GG's structural MRI showing clear damaged brain tissue in the occipital lobe, the fusiform gyrus, and the parahippocampal gyrus, unilaterally in the right hemisphere. (C) 3D Talairach cortical perfusion report showing hypoperfusion restricted to the internal parts of the right occipito-temporal cortex.

and Vanderwart (1980). GG correctly named 259 items on 260 (including animals, fruits, vegetables and man-made objects) in a total time of 8min55. In other words, he named each item at an average rate of 2 s, almost perfectly. Thus, GG clearly does not show any impairment in basic-level object recognition.

In contrast, standard neuropsychological tests showed a clear deficit for face processing, in line with the patient's self-reported complaints. The results showed impairments in perceiving and recognizing faces. First, GG obtained impaired scores in the Benton Facial Recognition Test (Benton, Sivan, Hamsher, Varney, & Spreen, 1983), more specifically showing difficulties in the second part of the test (in which the subject has to match faces presented under different viewpoints and lightings). Second, GG failed the faces subtest of the WMS-III (Weschler, 2001), revealing anterograde difficulties in encoding new faces. Finally, GG was impaired in a task of naming celebrities, underlying a defect in accessing the identity of well-known people via their face. This is a typical pattern of functional impairments in acquired prosopagnosia, as assessed by conventional neuropsychological tests.

The control neuropsychological assessment conducted three years later largely replicated these observations and showed an efficient global cognitive functioning (Table 2). Three new tasks of object perception (object decision, categorical judgment on different exemplars and categorical judgment on different viewpoints) showed preserved structural properties and abilities in perceiving objects across different viewpoints (even in non-canonical views). Concerning face recognition, a slight recovery was noticeable, but the patient still was impaired in the BFRT (Benton et al., 1983) and the WRMT (Warrington, 1984), and GG still reported the same difficulties with the recognition of familiar people in real life circumstances.

In summary, these results seem to point to a "pure" form of acquired prosopagnosia in patient GG. This provides us with a unique opportunity to explore in detail the nature of this patient's face recognition deficit, which may allow us in turn to shed light on theories of normal face perception and recognition.

Table 2
Patient GG's general neuropsychological assessment.

	November 2003	January 2007
General		
WAIS-R		
Verbal IQ	122	
Performance IQ	99	
Full-scale IQ	113	
Visual perception		
Visual object and space perception battery		
Shapes detection	20/20	20/20
Incomplete letters	20/20	20/20
Silhouettes	20/30	20/30
Object decision	16/20	16/20
Dot counting	10/10	10/10
Position discrimination	20/20	20/20
Number location	10/10	10/10
Cube analysis	10/10	10/10
Visual agnosia battery (PEGV)		
Entangled figures	10/10	
Figure decision	10/10	
Thurstone test	17 items in 4 min	
Hooper test	26/30	
Benton Line Orientation Test	28/30	30/30
Object decision (Delvenne et al., 2004)		170/176
Categorical objects judgment		
Different exemplars		37/40
Different viewpoints		35/40
Executive functioning		
Phonological verbal fluency	30	18
Trail Making Test		
Part A	0 err–27 s	0 err–43 s
Part B	0 err–115 s	0 err–86 s
Stroop Test		
Naming	0 err–86 items	
Reading	0 err–75 items	
Interference	0 err–50 items	
Wisconsin Card Sorting Test	6/6	
Praxis		
Clock Drawing Test		
Oral order	10/10	
Praxia Battery	30/30	
Rey-Osterreich Figure (copy)	31/36, 2 min 15	30/36, 2 min 20
Memory		
Working memory		
Forward span	6	6
Backward span	4	4
Spatial span (Block tapping)	6	
Verbal episodic memory		
Grober and Buschke 16 items		16; 5(16); 9(16); 12(15); r 48/48; DR 11(16)
WMS-III–verbal memory subtests		
Logical memory I	34; 16	
Visual episodic memory		
Rey-Osterreich figure (immediate recall)	12[a]	9[a]
Doors Test (Baddeley)	19/24	
DMS 48	43/48; 46/48	
WMS-III–Visual Memory Subtests		
Family scenes		17; 17
Visual reproduction		83; 59
Language		
Oral production		
Semantic verbal fluency	45	38
Naming (DO80)	80/80	80/80
Snodgrass and Vanderwart naming	259/260, 8 min 55	
Oral comprehension		
Pyramids and Palm Trees Test (visual)	52/52	
Written comprehension		
Text reading		80/80, 35 s
Reading of regular and irregular words	121/121	
Pyramids and Palm Trees Test (verbal)	52/52	
Faces		
Benton Facial Recognition Test (BFRT)	37/54[a]	36/54[a]
Memory of new faces		
WMS-III–Facial subtest	25/48[a]; 27/48[a]	34/48; 36/48
Warrington Recognition Memory Test (WRMT)		29/50[a]
Cambridge Face Memory Test (CFMT)		29/72[a] (collected in 2010)

Table 2 (*Continued*)

	November 2003	January 2007
Identification of famous people		
Familiarity judgment		37/50[a]
Identification from photographs	26/40[a]	35/40
Identification from names	39/40	
Age judgment	40/40	

[a] Indicates impaired scores (below 2 standard deviations from controls' score or under percentile 5).

3. Computer experiments

In total, GG was administered with a set of 24 behavioural experiments conducted in 2007. These experiments were conducted during two time periods, in January and August 2007. GG realized in average 5 tests per day. The order of administration was approximately the same than the order reported in the paper: GG began with tasks of faces and objects matching, then tasks of visual similarity and general global processing, then tasks of face detection and finally tasks of face holistic processing. In all 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. Percentages of correct responses and response times on correct trials were calculated. RTs that were longer than two SDs of the mean were discarded.

As means of comparison for GG's results, five to ten healthy control participants were selected for each experiment, controlling for gender, socio-economic background and age. 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. The number of control participants and their age differ slightly across the experiments. When GG performed as well or better than controls, we considered that five participants were sufficient to demonstrate normal processing. However, when his performance was below that of the five controls, we increased the number of participants to ensure that GG was truly impaired in that particular task.

For intra-subject and intra-group statistical analyses, we used respectively classical independent sample *t*-tests and paired sample *t*-tests. These analyses were conducted by SPSS 14.0 within the framework of one-tailed hypothesis (0.05 *p* value). To compare the results of GG to the control participants, we used the modified *t*-test of Crawford and Howell (1998) for single-case studies. This procedure decreases the type 1 error as it tests whether a patient's score is significantly below controls by providing a point estimate of the abnormality of the score. Here we used a 0.05 *p* value within the framework of a unilateral hypothesis. Consequently, all scores associated with a *p* value under 0.05 were considered as reflecting an abnormal result. 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).

Concerning the terminology used in this paper for various tasks, and to avoid semantic confusions as much as possible, definitions will be given for some words frequently appearing in the experiments and in this paper in general (following Sergent, 1989). A face *detection* task involves a decision as to whether or not a given stimulus is a face. A *discrimination* (or simultaneous matching) involves a comparison between two (or more) simultaneously presented items and a decision as to their sameness or difference. A *recognition* (or delayed matching) involves a judgment of previous occurrence and therefore whether an item – a face or an object –has been seen earlier. The comparison is thus between a presently generated representation and a stored representation. A *categorization* involves the classification of the object or face into a predetermined category, and different grains of resolution may be imposed on the process depending on the type of categorization (e.g., basic level *vs.* subordinate level). *Identification* is the categorization of a face as that of a unique individual whose identity must be accessed. Obviously, two of these terms can be valid to describe a given task, for instance a delayed matching task with a distractor is both a recognition and a discrimination/matching task. In this particular situation, both terms can be used.

3.1. *Experiments 1–4: face processing*

The first set of experiments aimed at characterizing better GG's impairment in face processing. We asked GG to identify famous faces with external features (experiment 1), without external features (experiment 2), to learn face photographs and perform an old/new recognition task (experiment 3), and match unfamiliar faces across viewpoint changes (experiment 4).

3.1.1. *Retrograde memory of faces: identification of celebrities*

3.1.1.1. Experiment 1. Faces with external cues. Rationale. The simplest and most objective way to identify a face recognition deficit is to test the patient with face photographs of people supposedly well-known by him. Typically, photographs of famous faces are used to assess this. Since semantic knowledge of famous people is variable across individuals, we carried out two experiments assessing the identification of famous faces which took into account the domains of interest of the patient and his previous cultural knowledge.

Material and procedure. To create a famous people recognition test adequate for GG, we selected fifty celebrities which would have been easily recognized by him prior to his stroke, according to his wife (actors, singers, politicians, sportsmen, . . . from the 1950 to 2000s). We selected color photographs on the web and presented the faces of these famous people with external cues (hair, earrings, parts of clothes, . . .). For each face presented one by one, GG was instructed to name the person, and when this was not possible to provide as much information as possible about each famous person. If not named, a famous person was considered to be correctly identified if at least three semantic attributes were accurately provided without any errors (nationality, profession and another specific element). The pictures subtended 10.6° in height and 8.5° in width, on a white background.

Control participants. Six healthy males were tested (mean age: 64.83; SD: 2.14).

Results. Surprisingly enough, GG obtained 86% of correct answers, which was in the normal range (mean: 88%; SD: 6.97; $t = 0.305$, $p = 0.39$) (Fig. 2). However, the patient spontaneously pointed to the fact that the pictures were very famous, indicating that he recognized the pictures rather than the actual faces of the celebrities. In fact, most of the selected photographs consisted of "iconographic" images, which had been overly and repetitively presented in the media (see Carbon, 2008). Consequently, a second task without external cues was presented to GG and to a group of controls participants.

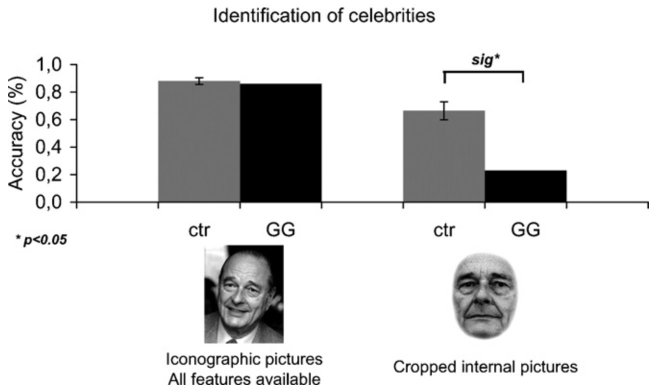

Fig. 2. Results of GG and age-matched controls in experiments 1 and 2: identification of celebrities, with and without external features. Bars represent standard errors.

3.1.1.2. Experiment 2. Faces without external cues. Material and procedure. The same 50 celebrities than in the previous task, together with 50 others selected with the help of GG's spouse, were used. The pictures selected were less common, and showed a neutral expression. Each face was cropped in order to present the internal features only (Fig. 2). Instructions, presentation and scoring were exactly the same as in the previous task.

Control participants. Nine healthy males were tested (mean age: 60.56; SD: 6.91).

Results. Here GG was massively impaired at identifying the celebrities. He identified only 23 faces out of 100, and was not very confident even when he answered correctly. Among the 43 personalities GG identified well in the previous task ("iconographic" pictures with external cues), he identified only 9 of them here. The task was also more difficult for controls but they still obtained quite good results overall (mean: 66.4%; SD: 19.5). GG was significantly impaired in comparison with normal controls ($t = 2.113$, $p < 0.05$) (Fig. 2).

3.1.1.3. Experiment 3. Anterograde memory for faces: old/new face recognition. Material and procedure. In this task participants were asked to learn thirty faces. Each face was presented during four seconds. Next, in a forced-choice task, the participant was presented with pairs of faces. For each pair, the participant had to decide which face belonged to the learnt list. The target and the correct probe stimuli were always two different front photographs of the same person. There was no time constraint. The stimuli were color uncropped face pictures (half female) subtending approximately 12° in height and 9.2° in width, on a white background. The distractor face was always chosen as having similar hairstyle and skin color as the target face (Fig. 3).

Control participants. Seven healthy males were tested (mean age: 65.86; SD: 3.34).

Results. Congruently with his results at the WRMT (Warrington, 1984; Table 2), GG was strongly impaired at this task (GG: 65.5%; mean: 86.7%, SD: 8.55; $t = 2.317$, $p < 0.05$). He was in the range of normal response times for the correct trials (GG: 2359 ms, mean: 2027 ms, SD: 541; $t = 0.574$, $p = 0.29$) (Fig. 3). These results confirm his difficulties in learning and recognition of photographs of new faces.

3.1.1.4. Experiment 4. Matching/discrimination of faces presented under different viewpoints. Material and procedure. In this experiment, we tested GG with a simultaneous matching task presenting faces under different viewpoints (one full front and two 3/4 profiles). GG was asked to match a full front target-face located on top of the display with one of the two 3/4 profile faces. One full front

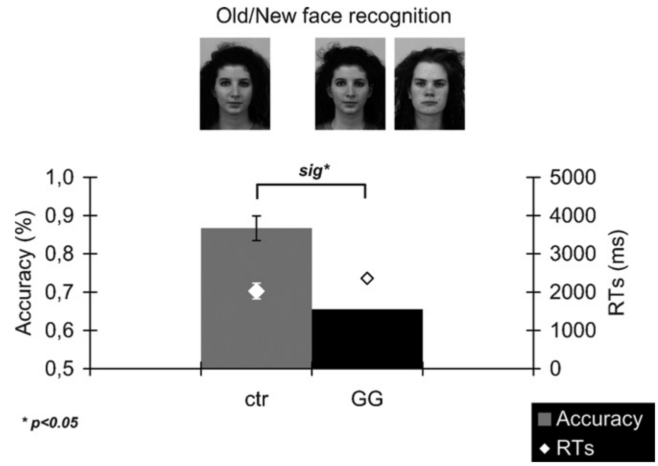

Fig. 3. Results of GG and age-matched controls in experiment 3: memory for new faces. Bar represents standard error.

and two 3/4 profile color photos cropped without external cues of sixteen individuals (eight women) were used. The experiment was divided into two blocks of 32 randomly presented trials. The stimuli subtended approximately 7.1° in height and 5.7° in width, on a white background.

Control participants. Seven healthy males were tested (mean age: 65.86; SD: 3.34).

Results. GG was impaired in comparison to the controls (GG: 68.7%; mean: 87.9%, SD: 6.61; $t = 2.717$, $p < 0.05$). He responded as fast as the controls in the trials he succeeded (GG: 3297 ms, mean: 2902 ms, SD: 826; $t = 0.447$, $p = 0.33$). These observations confirm the perceptual face processing impairment observed in the BFRT (Benton et al., 1983; Table 2) (Fig. 4).

Overall, this first set of experiments clearly confirms the existence of prosopagnosia in patient GG. The patient is significantly impaired at identifying famous faces, he is unable to learn and recognize new faces, and he is unable to match/discriminate unfamiliar faces presented under different viewpoints.

3.2. Is GG's impairment limited to faces? Experiments 5–8

While the majority of patients have problems with object recognition (e.g., HJA, Riddoch & Humphreys, 1987; LH, Levine &

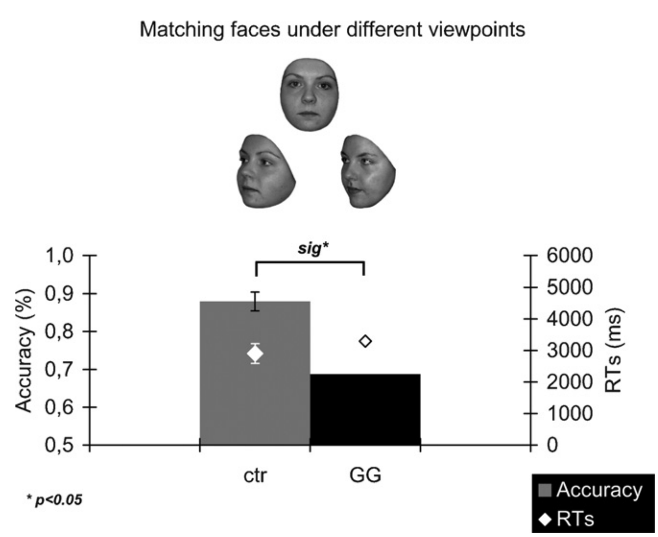

Fig. 4. Results of GG and age-matched controls in experiment 4: matching faces presented under different viewpoints. Bar represents standard error.

Calvanio, 1989; AR, Saumier et al., 2001; SM and RN, Behrmann & Kimchi, 2003; NS, Delvenne et al., 2004), other patients do not have such problems (see Table 1 for review). Yet, opponents of the specificity hypothesis in prosopagnosia (e.g., Beyn & Knyazeva, 1962; Bornstein, 1963; Damasio et al., 1982; Gauthier et al., 1999; Lhermitte et al., 1972) have raised the hypothesis, suggested originally by Faust (1955), that what characterizes prosopagnosia is a particular problem in recognizing or discriminating objects that are visually similar, rather than faces in particular. This line of reasoning originates from the observation that human faces – at least for a given gender and race – are very similar in shape and surface reflectance (color, texture). Moreover, while most objects have simply to be categorized at a basic-level ("it's a chair") or just a few exemplars have to be identified ("it's my car"), faces *have to* be individualized, a process which goes beyond the basic-level categorization of a visual stimulus as "a face" (face detection). In fact, face detection does not appear to cause a great deal of problems for many prosopagnosic patients (see next section). There are some variants of this view of prosopagnosia, but they all state that prosopagnosia is a problem at recognizing/discriminating items that are visually similar (Damasio et al., 1982; Gauthier et al., 1999). What is the current evidence supporting this view?

The specificity of the deficit in prosopagnosia has usually been tested by asking to categorize items belonging to visually similar superordinate categories (fruits, flowers, animals, ...), or to discriminate among exemplars of the same category (matching/forced choice discrimination tasks).

First, in categorization tasks, patients have been tested with pictures of: *fruits and vegetables* (e.g., Arguin, Bub, & Dudek, 1996; Barton, 2008a; De Renzi et al., 1994; Henke et al., 1998; Lopera & Ardila, 1992; Riddoch & Humphreys, 1987; Riddoch et al., 2008; Schweinberger et al., 1995; Sergent & Villemure, 1989; Stephan, Breen, & Caine, 2006); *animals* (e.g., Damasio et al., 1982; Lhermitte et al., 1972; Lopera & Ardila, 1992; Riddoch & Humphreys, 1987; Schweinberger et al., 1995; Shuttleworth, Syring, & Allen, 1982; Steeves et al., 2006; Tiberghien & Clerc, 1986; Wada & Yamamoto, 2001); *makes of cars* (e.g., Davidoff et al., 1986; De Haan, Young, & Newcombe, 1987; De Renzi et al., 1994; Henke et al., 1998; Lhermitte et al., 1972; Lopera & Ardila, 1992; McNeil & Warrington, 1991; Schweinberger et al., 1995; Sergent & Signoret, 1992a; Stephan et al., 2006; Young, De Haan, & Newcombe, 1990); *flowers* (e.g., Davidoff et al., 1986; De Haan et al., 1987; Lopera & Ardila, 1992; McNeil & Warrington, 1991; Sergent & Signoret, 1992a; Young et al., 1990); or *coins* (De Renzi et al., 1991, 1994; Spillmann et al., 2000). Some patients have also been asked to identify *famous buildings and places* (De Renzi, 1986a; De Renzi et al., 1994; McNeil & Warrington, 1991; Wada & Yamamoto, 2001). Even though the majority of prosopagnosic patients performed below normal range at these tasks, some of them succeeded, as mentioned in the introduction (see also Table 1): this was the case for patients VA (De Renzi et al., 1991); WJ (McNeil & Warrington, 1991); OR (De Renzi et al., 1994); MT (Schweinberger et al., 1995); WL (Spillmann et al., 2000); the patient of Wada & Yamamoto (2001); FB (Riddoch et al., 2008); 009 (Barton, 2008a); and DC (Rivest et al., 2009).

Second, matching/discrimination or recognition (delayed matching) tasks with visually similar items were tested in several studies with different kinds of stimuli: *pairs of glasses* (Buxbaum et al., 1996; De Renzi & di Pellegrino, 1998; Farah, Levinson, & Klein, 1995); *shoes* (De Gelder & Rouw, 2000a); *houses* (De Gelder & Rouw, 2000a); *snowflakes* (Gauthier et al., 1999); a set of *birds*, *cars*, *chairs* and *boats* (Schiltz et al., 2006); and different sets of novel objects, *Greebles* (Gauthier et al., 1999), *Scott objects* (Rossion et al., 2003), *Geons* (Behrmann, Peterson, Moscovitch, & Susuki, 2006), and *Fribbles* (Behrmann & Williams, 2007). While some patients were impaired in these experiments (Behrmann et al., 2006; Behrmann & Williams, 2007; De Gelder & Rouw, 2000a; Gauthier et al., 1999), others performed in the normal range: the three patients tested with pairs of glasses scored in the normal range (Buxbaum et al., 1996; De Renzi & di Pellegrino, 1998; Farah, Levinson, et al., 1995), and PS succeeded in the task with the *Scott objects* (Rossion et al., 2003) and could recognize individual items of birds, cars, chairs and boats in a delayed presentation mode accurately and rapidly (Schiltz et al., 2006).

In light of these observations, the interpretation of prosopagnosia as a problem at categorizing or discriminating items that are visually similar (Damasio et al., 1982; Gauthier et al., 1999) does not appear to be currently well supported. Moreover, most cases who have been characterized as having difficulties with visually similar nonface objects already showed massive problems at categorizing objects that had clear distinctive shapes (e.g., patients 1, 2 and 3; Damasio et al., 1982; RB, Davidoff et al., 1986; PH, De Haan et al., 1987; HJA, Riddoch & Humphreys, 1987; LH, Farah, Wilson, et al., 1995; SM, Gauthier et al., 1999; CR, Gauthier et al., 1999; Marotta, McKeeff, & Behrmann, 2002; DF, Steeves et al., 2006). Finally, the claim that these patients' impairments increase relatively more than normal observers when visual similarity of a distractor item increases (Gauthier et al., 1999) is not supported by strong evidence (see Busigny et al., 2010).

Nonetheless, this view remains influential because, in cases who have been reported to present with an impairment restricted to the category of faces, the investigation with visually similar nonface objects was not thorough and systematic, and generally did not take into account patients' speed (e.g., Barton, 2008a; Buxbaum et al., 1996; De Renzi et al., 1991, 1994; McNeil & Warrington, 1991; Riddoch et al., 2008; Rivest et al., 2009; Schweinberger et al., 1995; Spillmann et al., 2000; Wada & Yamamoto, 2001).

GG does not have any basic-level categorization difficulties, even with items belonging to visually similar categories. In the next experiments, we tested him in tasks that require face and object recognition at the individual level, taking into account both accuracy rates and speed. Moreover, contrary to previous studies (e.g., Gauthier et al., 1999) but in line with our recent investigation of the patient PS (Busigny et al., 2010), we manipulated visual similarity objectively and parametrically both with objects and faces (experiments 7 and 8).

3.2.1. Experiment 5. Face and object discrimination at the individual level

Material and procedure. The patient and control participants were presented with individual pictures from different object categories: birds, boats, cars, chairs and faces (see Schiltz et al., 2006). In a delayed two-alternative forced choice decision task, they were first presented with a target stimulus belonging to one of the five categories for one second. After an ISI (white screen) of the same duration, two probe stimuli (target and distractor) appeared, among which they were asked to indicate which one had been previously presented. To encode the response, participants were 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. The distractor belonged to the same (intra-category discrimination) or to another category (inter-category discrimination). Photographs of faces were cropped (the external cues were removed) and for all objects any "external" cue was also removed (e.g., license plates of the cars). Twenty-four gray scaled pictures of each category were used in the two conditions (inter- and intra-category). The experiment was divided into four blocks of 60 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.

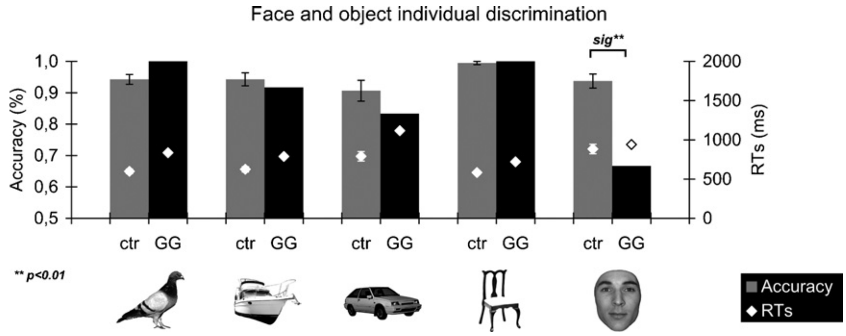

Fig. 5. Results of GG and age-matched controls in experiment 5: face and object discrimination at the individual level. Bars represent standard errors.

Control participants. Eight healthy males were tested (mean age: 66.25; SD: 3.28).

Results and discussion. For the between-category discrimination, performance was at ceiling for all the participants and for all the categories (global performance of GG: 99.2%; mean: 99.3%, SD: 0.29; t = 0.325, p = 0.38). In the within-category discrimination, GG performed in the normal range for the four non-face categories: birds (GG: 100%; mean: 94.3%, SD: 4.42; t = 1.222, p = 0.13), boats (GG: 91.7%; mean: 94.3%, SD: 5.87; t = 0.418, p = 0.34), cars (GG: 83.3%; mean: 90.6%, SD: 9.38; t = 0.734, p = 0.24), and chairs (GG: 100%; mean: 99.5%, SD: 1.47; t = 0.334, p = 0.37). However, GG was massively impaired for faces (GG: 66.7%; mean: 93.8%, SD: 6.30; t = 4.053, p < 0.01) (Fig. 5). Concerning response times, GG was slightly slower that the controls for all categories but the difference did not reach significance, except for the category of birds (GG: 836 ms; mean: 598 ms, SD: 88; t = 2.55, p < 0.05). However, GG's performance with these pictures was better than that of controls (Fig. 5), so that this slowing down may be accounted for in terms of a speed–accuracy trade-off. When computing an inverse efficiency measure (average response times of the correct trials divided by accuracy; Townsend & Ashby, 1983), GG scored in the low but normal range (GG: 836; mean: 638, SD: 117; t = 1.587, p = 0.08). Moreover, the fact that the task was easy for the controls, who responded extremely rapidly, and the fact that one item always appeared in GG's blind visual field (due to his complete left hemianopsia), may have prevented the patient to respond as fast as the controls in this experiment. Nevertheless, to ensure that GG does not present with particular difficulties in matching birds, and following one of the reviewers' suggestion on a previous version of this paper, we tested GG in an additional task. We used 56 new pictures of birds that were paired two by two (for example, two pigeons of the same size and the same orientation). We presented first the target in the middle of the screen during 1000 ms and we presented the two probes in the right visual field of the patient during unlimited time, one above and one below. This time, GG obtained a percentage of correct responses of 94.8% in an average correct response time of 1026 ms. Five age-matched control participants (average age: 66.4) obtained an accuracy of 97.2% (SD: 2.61; t = 0.842, p = 0.22), and an average correct response time of 1156 ms (SD: 292; t = 0.406, p = 0.35). These results showed that GG is capable to realize the task as well as controls and that the small slowing down observed in experiment 5 did not reflect particular difficulties in bird matching.

Overall, the results of this experiment strongly support the specificity of GG's impairment for face processing. Importantly, this specific impairment cannot be attributed to a larger difficulty for recognizing faces than objects, since faces were not processed worse or slower than the other object categories by control participants (Fig. 5).

3.2.2. Experiment 6. Identification of famous buildings and monuments

Material and procedure. As for the famous people test, we selected 30 famous buildings and monuments well-known by the patient (e.g., Eiffel Tower, Pisa Tower, Statue of Liberty). The colored photographs were selected from the web and were presented one-by-one in the same size in the center of the screen. Participants were asked to name the 30 monuments, and when they were not successful to provide as much information as possible about each of them. An item was considered to be correctly identified if it was named or if at least two correct semantic attributes were provided (including the city where the monument or the building was located). The stimuli subtended $12^\circ \times 16^\circ$ on a white background.

Control participants. Five healthy males were tested (mean age: 66; SD: 2.83).

Results. GG was very efficient at identifying famous monuments and buildings. He provided the correct name for 27 of the 30 items, well above the normal range in terms of accuracy (GG: 90%; mean: 89.3%, SD: 13.82; t = 0.044, p = 0.48) and significantly faster than the controls (GG: 4349 ms; mean: 7186 ms, SD: 543; t = 4.769, p < 0.01) (Fig. 6).

3.2.3. Experiment 7. Discrimination of gradually similar objects

Material and procedure. This task was aimed to evaluate the ability of participants to discriminate pictures of cars through different levels of similarity (see Busigny et al., 2010). Morphed pictures of cars were generated with a morphing Software (Morph^{TM}). Twenty pictures of cars were used and were morphed two-by-two. From

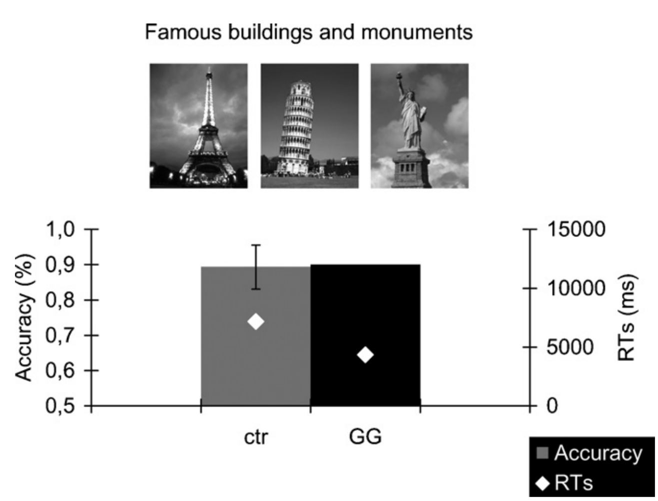

Fig. 6. Results of GG and age-matched controls in experiment 6: identification of famous buildings and monuments. Bar represents standard error.

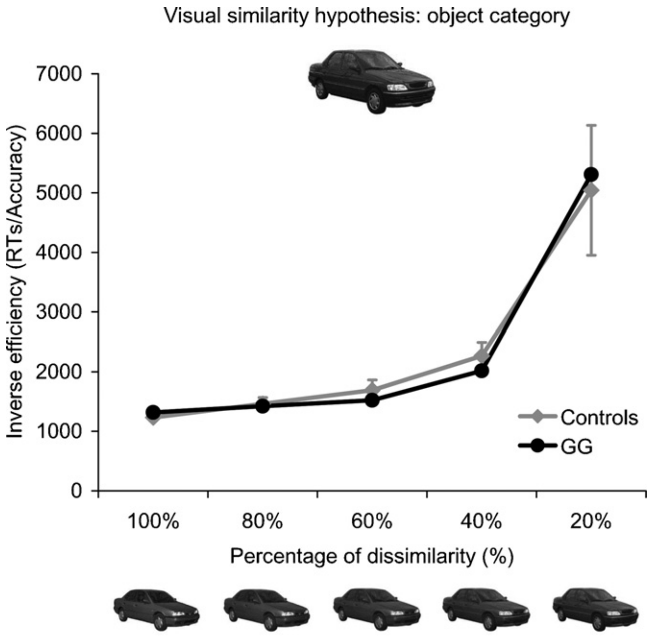

Fig. 7. Results of GG and age-matched controls in experiment 7: discrimination of gradually similar objects. Results are displayed in inverse efficiency measures (correct RTs divided by accuracy rates). Bars represent standard errors.

each original picture of car, we created five levels of morphing, which reflected five levels of (dis)similarity (20, 40, 60, 80 and 100%) (Fig. 7). The task was a delayed two-alternative forced choice. The target was presented first during 2000 ms, followed by an ISI (1000 ms) and then a screen appeared showing the target accompanied with one distractor. This distractor consisted of one of the five levels of morphing of the target car. The participant had to decide which one of the two probe pictures was the same as the previous one, by pressing a corresponding key. The experiment was divided into three blocks of 50 randomized trials. The stimuli subtended approximately $5.7^\circ \times 12.7^\circ$ on a white background. Participants were expected to perform better and faster with the most dissimilar distractors, with a progressive increase of error rates and RTs as the visual similarity between the target and distractor increased. If visual similarity accounts for GG's face processing impairment, the slope reflecting the increase in error rates and correct RTs should be steeper in GG than in normal controls (i.e. interaction between the degree of similarity of the distractor and the group).

Control participants. Six healthy males were tested (mean age: 64.83; SD: 2.14).

Results and discussion. Accuracy rates and RTs are reported separately in Table 3 for GG and control participants, for all levels of visual dissimilarity between the target and the distractor. Overall, GG performed as well as controls (GG: 82.74%; mean: 84.68%, SD: 4.72; $t = 0.381$, $p = 0.36$) and was also as fast as them (GG: 1607 ms; mean: 1923 ms, SD: 657; $t = 0.445$, $p = 0.34$). He obtained normal accuracy rates and response times for each level of dissimilarity (Fig. 7). For the most difficult level, in which the dissimilarity between the target and the distractor is only of 20%, GG scored at chance level, as did three of the controls. Next, statistical comparisons were performed on inverse efficiency in order to control for trade-off between the two measures. As expected, the control participants showed an increased slope (RTs/accuracy) with the degree of dissimilarity: the more similar the distractor was to the target (from 100% difference to 20% difference), the less efficient the controls were (Fig. 7). The decrease in performance with decreasing levels of dissimilarity was also noticeable for accuracy and response times considered separately (Table 3). GG obtained exactly the same results as the controls. At each level, his accuracy and correct response times were in the normal range and his inverse efficiency pattern followed exactly the same slope as the controls (100%: $t = 0.895$, $p = 0.21$; 80%: $t = 0.145$, $p = 0.45$; 60%: $t = 0.366$, $p = 0.37$; 40%: $t = 0.415$, $p = 0.35$; 20%: $t = 0.091$, $p = 0.47$) (Fig. 7).

3.2.4. Experiment 8. Discrimination of gradually similar faces

Rationale. A prediction of the visual similarity account of acquired prosopagnosia is that patients have relatively more difficulties discriminating/recognizing items that are visually similar than visually dissimilar, irrespective of the domain. Hence, even within the face domain, these patients should suffer relatively more when the individual faces that need to be discriminated are extremely similar. However, if their impairment rather reflects impaired processes that are specialized for face stimuli, patients should be impaired at all levels of visual similarity for faces, although they may be relatively less impaired when faces that require to be discriminated are extremely different (very easy) or extremely similar (very difficult, even for normal controls). We contrasted these predictions with a 2AFC task in which the physical similarity of the distractor and the target was manipulated parametrically, similarly to the previous task.

Material and procedure. To create the test, we followed the same procedure as for the cars. Thirty-two color scanned pictures of faces (from the Max-Planck Institute, Germany) were used (half female) and were morphed two-by-two using a technique for modeling textured 3D faces (Morphable Model for the Synthesis of 3D Faces; Blanz & Vetter, 1999). As for the pictures of cars, we employed five levels of (dis)similarity (20, 40, 60, 80 and 100%) (Fig. 8). Overall, we used 64 trials for each level. The task and the instructions were the same as in the previous experiment. The experiment was divided into five blocks of 64 randomized trials. The stimuli subtended approximately $7.8^\circ \times 6.4^\circ$ on a white background.

Control participants. Seven healthy males were tested (mean age: 65.71; SD: 2.29).

Results and discussion. As for the previous experiment, accuracy rates and RTs are reported in Table 4, for GG and control participants, at all levels of visual dissimilarity between the target and the distractor. Overall, GG scored in the normal range (GG: 83.44%; mean: 86.47%, SD: 3.9; $t = 0.727$, $p = 0.25$) and was not significantly slower than normal controls (GG: 1449 ms; mean: 1231 ms, SD: 209; $t = 0.976$, $p = 0.18$). However, GG was significantly impaired

Table 3
GG's accuracy rates and response times for the experiment 7: visual similarity hypothesis, object category.

	Accuracy (%)				RTs (ms)			
	ctr	GG	*t*	*p* (one-tailed)	ctr	GG	*t*	*p* (one-tailed)
100%	98.48 (3.71)	100.00	0.379	0.36	1215 (106)	1319	−0.908	0.20
80%	96.08 (6.08)	100.00	0.597	0.29	1403 (248)	1424	−0.078	0.47
60%	89.78 (5.56)	90.32	0.090	0.47	1510 (353)	1377	0.349	0.37
40%	81.71 (9.73)	85.37	0.348	0.37	1843 (484)	1723	0.230	0.41
20%	57.33 (10.93)	38.00	−1.637	0.08	2918 (1612)	2017	0.517	0.31
Overall	84.68 (4.72)	82.74	−0.381	0.36	1923 (657)	1607	0.445	0.34

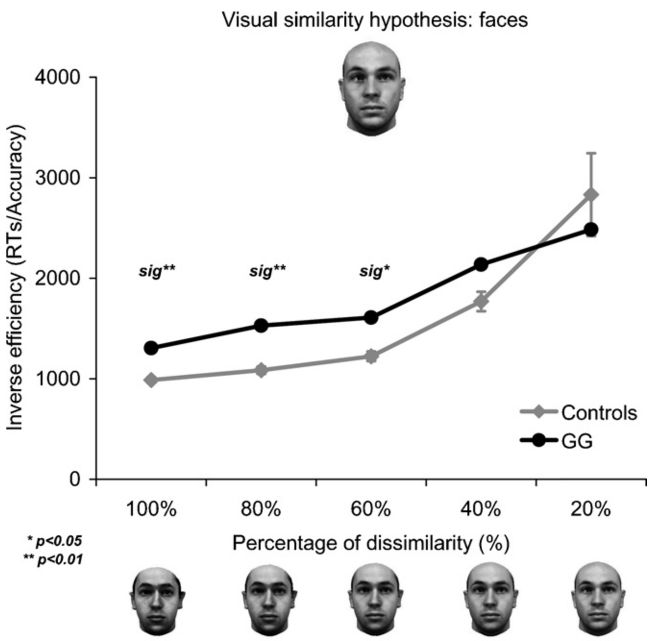

Fig. 8. Results of GG and age-matched controls in experiment 8: discrimination of gradually similar faces. Results are displayed in inverse efficiency measures (correct RTs divided by accuracy rates). Bars represent standard errors.

in accuracy at the two first levels (100%: $t = 4.477$, $p = < 0.01$; 80%: $t = 6.070$, $p < 0.01$). GG presented also a significant slowdown relative to controls at the three first levels (100%: $t = 3.312$, $p < 0.01$; 80%: $t = 2.679$, $p < 0.05$; 60%: $t = 1.991$, $p < 0.05$) (Table 4).

Control participants' efficiency decreased progressively as similarity between the target face and its distractor increased, just as they performed with pictures of cars (Fig. 8). However, GG's pattern of results with faces was strikingly different from his performance with pictures of cars. First, GG was impaired relative to controls in some conditions. Second, his impairment concerned the three first levels of dissimilarity. The analyses of inverse efficiency confirmed that GG was impaired for the levels of dissimilarity of 100% ($t = 3.851$, $p < 0.01$), 80% ($t = 4.272$, $p < 0.01$) and 60% ($t = 2.866$, $p < 0.05$), that is, when the task was the easiest for the control participants. However, when the faces needing to be discriminated became very similar, there was no significant difference between GG and controls in terms of efficiency (last two levels: 40%: $t = 1.339$, $p = 0.11$; 20%: $t = 0.298$, $p = 0.39$) (Fig. 8).

Together with the results of experiment 7, these observations do not support the account of prosopagnosia in terms of impairment in processing visually similar items (Damasio et al., 1982; Faust, 1955; Gauthier et al., 1999). In fact, if anything, relative to controls, the patient's impairment was most spectacular when the faces to discriminate were clearly dissimilar. If prosopagnosia were due to a difficulty in processing items that are visually similar, one would expect that GG's difficulties would increase more than controls as similarity increases. That was not the case at all: the easiest levels of face discrimination were failed by GG, but, if anything, the most difficult ones were not. Admittedly, we cannot exclude that this pattern of results for the most difficult discriminations may be due to a floor effect (the control participants performed 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: 63% of correct responses for normal participants) and increase of response times. Also, it might be that with a larger number of controls, GG's performance would also be significantly lower than normal controls at discriminating highly similar faces. Nevertheless, one can safely conclude from these observations that the patient's performance is not more affected by increases of visual similarity between a target face and its distractor as compared to normal observers.

Altogether, the four experiments of this section show that GG presents with normal abilities at processing visually similar items of nonface categories. Consequently, GG's prosopagnosia cannot be accounted for in terms of impaired processing of visually similar items. If GG's prosopagnosia is not a problem at disambiguating items that are visually similar, alternatives explanations need to be considered. One possibility is that in order to disambiguate highly similar stimuli, GG may operate by detecting a specific feature, a detail, or a unique property rather than relying on a global and integrated representation of the visual stimulus. In the next section, we first test GG's holistic processing of nonface objects at the level of feature integration.

3.3. General visual integrative abilities: experiments 9–14

In this section, we were interested in assessing the general visual integrative abilities of GG, that is, *holistic processing* as defined by the Gestalt theory (cfr. Section 1). We used non-face stimuli because we believe that it is critical to avoid confounding general integrative abilities with holistic face processing. As mentioned in Section 1, the idea that prosopagnosia may be interpreted in terms of a general defect of visual integrative processes was put forward by Levine and Calvanio (1989), in their investigation of acquired prosopagnosic patient LH. These authors showed that LH performed badly in tasks of visual closure, which required identifying visual items presented in an incomplete form or embedded in visual white noise (gestalt completion, concealed words, snowy pictures, see Levine & Calvanio, 1989).

Similarly, Riddoch and Humphreys (1987) showed that HJA, who also suffered from prosopagnosia and a lack of holistic processing (Boutsen & Humphreys, 2002) did not present the classical Navon interference effect (see below). They interpreted the problem of HJA as reflecting *an impairment in integrating local part information with information about global shape, in that local parts are treated separately and not grouped together to elaborate the global shape description* (Riddoch & Humphreys, 1987). Many other stud-

Table 4
GG's accuracy rates and response times for the experiment 8: visual similarity hypothesis, faces.

	Accuracy (%)				RTs (ms)			
	ctr	GG	t	p (one-tailed)	ctr	GG	t	p (one-tailed)
100%	99.33 (0.84)	95.31	−4.477	0.00**	981 (74)	1243	−3.312	0.00**
80%	98.21 (1.41)	89.06	−6.070	0.00**	1066 (103)	1361	−2.679	0.02*
60%	93.30 (3.46)	87.50	−1.568	0.08	1142 (125)	1408	−1.991	0.04*
40%	78.57 (8.15)	76.56	−0.231	0.41	1387 (222)	1636	−1.049	0.17
20%	62.95 (10.85)	68.75	0.500	0.32	1786 (832)	1708	0.088	0.47
Overall	86.47 (3.90)	83.44	−0.727	0.25	1231 (209)	1449	−0.976	0.18

* $p < 0.05$.
** $p < 0.01$.

ies have used tests of visual closure to assess the global configural processing in prosopagnosic patients, using for example the *Street figure-completion test* (Street, 1931), the *Gollin incomplete pictures* (Gollin, 1960), the *Kanisza triangles* (Kanizsa, 1955), or the *Navon hierarchical letters* (Navon, 1977). The large majority of acquired prosopagnosic patients tested with these tasks were impaired (e.g., Behrmann & Kimchi, 2003; De Renzi, 1986a, 1986b; De Renzi et al., 1991; Lê et al., 2002). However, these patients, including LH and HJA, suffered from marked deficits for object recognition, that is, their impairment reflects general visual integrative agnosia.

In contrast, several cases of acquired prosopagnosia with no object recognition deficit succeeded in tasks of visual closure: three patients studied by De Renzi and colleagues [patient no. 4 (De Renzi, 1986a), VA (De Renzi et al., 1991) and Anna (De Renzi & di Pellegrino, 1998)] who presented no impairment in the Street's completion test concomitantly with no apparent objects recognition impairment. Another case of prosopagnosia with no general visual agnosia, MT (Henke et al., 1998), also succeeded the Street's completion task. In a recent study, Barton (2009) also showed in a group study of acquired prosopagnosic patients a general normal *Navon effect* for the group (main effect of the global level and main effect of the local level). However, the patients were significantly slowed down in comparison with the controls and the individual data of the patients were not provided (see Busigny & Rossion, in press).

Thus, even though some studies tend to show that general Gestalt/holistic processing can be preserved in prosopagnosia, they are rare. Here, we investigated more extensively the general visual integrative abilities of GG. Our prediction was that the patient would succeed the three following experiments and show intact general integrative/configural processing of non-face objects.

3.3.1. Experiment 9. Navon effect

Rationale. In his original paper, Navon (1977) tested the hypothesis that perceptual processes proceed from global structuring towards more and more fine-grained analysis, a theory that he termed *global addressability*, and which is inspired from earlier studies on object perception under the Gestaltist approach (Flavell & Draguns, 1957). To test this theory, he created hierarchical letters, in which global letters are composed with small letters. He showed that normal observers process the global level better, and that the processing of the local level is influenced by the global level.

Material and procedure. This task was inspired by the study of Behrmann, Avidan, Marotta, and Kimchi (2005). The stimuli were four hierarchical letters of two types: consistent and inconsistent letters. In the consistent letters, the global and the local letters were identical (i.e. a large H made of smaller Hs and a large S made of small Ss). In the inconsistent letters, the global and the local letters were different (i.e. a large H made of smaller Ss and a large S made of smaller Hs). Each stimulus was presented one by one with the instruction to identify either the global letter, or the local letter, by pressing a corresponding key. A 500 ms ISI and a 500 ms fixation cross preceded each trial. The experiment was divided into four blocks of 48 consistent and inconsistent randomized trials. In the blocks 1 and 3 the instructions were to identify the global letter, in the blocks 2 and 4, the instructions were to identify the local letters. The global letters subtended 3.2° in height and 2.3° in width, and the local letter subtended 0.53° in height and 0.44° in width.

Control participants. Five healthy males were tested (mean age: 66; SD: 2.83).

Results. First, regarding accuracy, all control participants as well as GG achieved ceiling performance. Through the four conditions, the age-matched controls succeeded with 99.4% and GG made no mistake (100% in each condition).

Next, concerning the correct RTs, as it is typically demonstrated (Navon, 1977), the age-matched controls showed an interference effect in the local condition: the identification of the smaller letter was influenced by the large one, the performance being significantly lower when the global and the local letters were inconsistent (local consistent mean: 1044 ms, SD: 330; local inconsistent mean: 1165 ms, SD: 337; $t_4 = 2.766$, $p < 0.05$) (Fig. 9A). We also found an interference effect in the global condition: the identification of the large letter was influenced by the smaller ones, the performance being significantly lower when the global and the local letters were inconsistent (global consistent mean: 1029 ms, SD: 173; global inconsistent mean: 1108 ms, SD: 248; $t_4 = 2.262$, $p < 0.05$) (Fig. 9B). In his first study, Navon did not find this effect (Navon, 1977), but it was found in subsequent studies (e.g., Barton, 2008b, 2009; Behrmann et al., 2005; Busigny & Rossion, in press). As in Behrmann et al. (2005), there was no statistical difference between local and global conditions ($t_4 = 0.890$, $p = 0.21$).

Regarding GG's response times, they were in the normal range and in fact the patient's RTs were slightly faster than those of the age-matched controls in the local conditions (consistent: 613 ms, $t = 1.192$, $p = 0.15$; inconsistent: 666 ms, $t = 1.352$, $p = 0.12$) and in the global conditions (consistent: 749 ms, $t = 1.477$, $p = 0.11$; inconsistent: 840 ms, $t = 0.986$, $p = 0.19$) (Fig. 9A and B). Second, GG was significantly sensitive to the interference both in the local condition ($t_{94} = 1.916$, $p < 0.05$) and in the global condition ($t_{94} = 2.062$, $p < 0.05$).

Third, we computed indexes of interference using the formula [(consistent − inconsistent)/(consistent + inconsistent)] for both the global and local conditions. GG obtained exactly the same interference indexes as the age-matched controls in the local condition (GG: 4.17%; mean: 5.61%, SD: 3.97; $t = 0.331$, $p = 0.38$) and in the global condition (GG: 5.74%; mean: 3.22%, SD: 3.17; $t = 0.726$, $p = 0.25$).

Finally, we compared the global and local conditions between each other. The age-matched controls did not present any difference between the two conditions (Global mean: 1068 ms, Local mean: 1105 ms; $t_4 = 0.293$, $p = 0.39$). GG was significantly faster in the local condition (Global mean: 794 ms, Local mean: 639 ms; $t_{190} = 5.841$, $p < 0.001$), which is somewhat unusual. Nevertheless, when we compared the indexes of difference between the two conditions for each control (local and global), GG was not different from the age-matched controls ($t = 0.884$, $p = 0.21$) (Fig. 9C). Some of the participants were faster in the global condition, but others were faster in the local condition (as was also the case in Behrmann et al., 2005). Finally, contrary to the cases of congenital prosopagnosia of Behrmann et al. (2005) who showed an "*asymmetric local-to-global interference*" (i.e. an exaggerated slowing down in the global condition when the stimuli are inconsistent), GG showed the same magnitude of effect in the local and the global conditions (no interaction effect between Condition × Congruency: $F(1, 191) = 0.522$, $p = 0.24$).

Overall, these results show that GG is able to derive normally a global configuration from the organization of local elements, suggesting that he has preserved general visual integrative abilities.

3.3.2. Experiments 10–12. Detection and discrimination of possible/impossible 3D figures

Rationale. Here we presented a new experiment to the patient GG and controls, requiring the integration of features in a complex 3D representation. We used line drawings of complex volumetric 3D figures (Williams & Tarr, 1997), in which the lines formed an object that was either structurally possible in 3D, or impossible (Fig. 10, see the full set of objects on http://titan.cog.brown.edu:8080/TarrLab/stimuli). This task is inspired from a study by Ratcliff and Newcombe (1982), and requires the integration of multiple lines in space, to form a coherent percept of a three-dimensional (3D) object

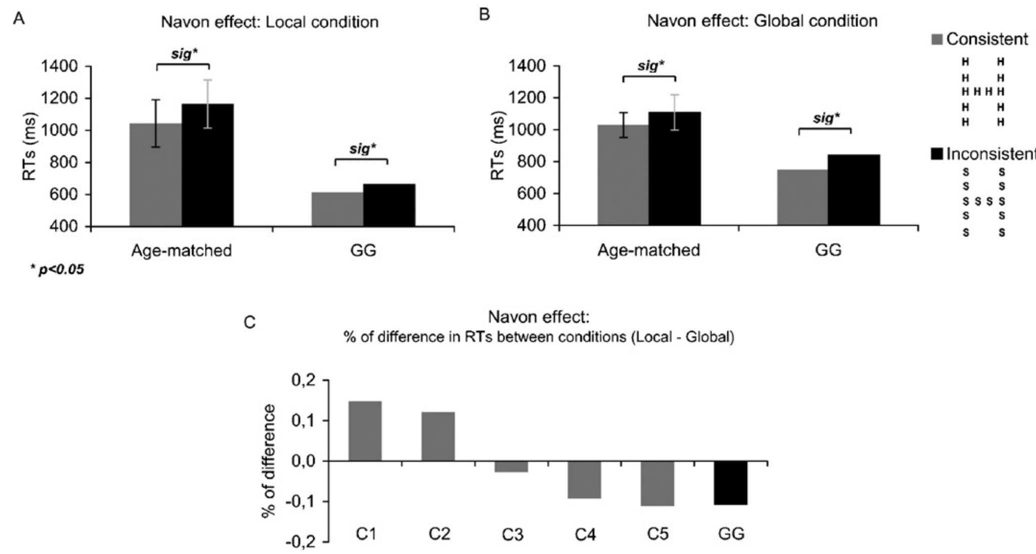

Fig. 9. Results of GG and age-matched controls in experiment 9: Navon effect. (A) Local condition. (B) Global condition. (C) Percentage of difference in RTs between local and global conditions. Bars represent standard errors.

For normal observers, the structural impossibility of some of these figures is perceived rapidly, without having to check every single line joints for any incoherence. Interestingly, we showed previously that a prosopagnosic patient with general integrative visual agnosia (NS, Delvenne et al., 2004) was impaired at the possible/impossible detection task with these stimuli. Here, we expect that GG would succeed at this task.

Material and procedure. The first experiment was to decide whether the drawings were structurally possible (i.e. if they could exist in real life) or not. Each drawing was presented one-by-one and the participant had to decide if each drawing was possible or impossible by pressing a corresponding key. Eighty possible and 80 impossible figures were presented randomly in two blocks. We added two experiments with these stimuli, in which the task was to match a target drawing (on top of the display) to one of two drawings presented below, at an orientation in depth that was different than the target (Fig. 10). Thus, the experiment required a two-alternative forced choice. The first matching task was composed of 40 possible figures and the second one of 40 impossible figures. In the three tasks, the stimuli subtended approximately $9.2^{\circ} \times 9.2^{\circ}$ on a white background.

Control participants. Five healthy males were tested (mean age: 66; SD: 2.83).

Results. For the possible/impossible detection task, GG obtained excellent results, being at least as accurate as the controls (GG: 91.9%; mean: 81.5%, SD: 10.7; $t = 0.886$, $p = 0.21$) and as fast as them (GG: 2557 ms; mean: 3464 ms, SD: 2217; $t = 0.373$, $p = 0.36$) (Fig. 10A).

In the matching task of possible figures, GG was also as accurate (GG: 97.5%; mean: 98%, SD: 1.12; $t = 0.408$, $p = 0.35$) and as fast (GG: 4035 ms; mean: 3882 ms, SD: 1300; $t = 0.107$, $p = 0.46$) as the controls. This was also found for impossible figures, for accuracy (GG: 95%; mean: 95.5%, SD: 3.26; $t = 0.140$, $p = 0.45$) and correct response times (GG: 4837 ms; mean: 4263 ms, SD: 1549; $t = 0.338$, $p = 0.38$) (Fig. 10B). Interestingly, both the normal controls and GG were slightly less accurate and were slower (but not significantly) at matching structurally impossible than possible figures (Fig. 10B), in line with the literature (e.g., Soldan, Hilton, & Stern, 2009; Williams & Tarr, 1997). Thus, once again, patient GG, contrary to previous cases of prosopagnosia who also presented object recognition defects (e.g., Delvenne et al., 2004), appears to be sensitive to the structural integrity of these stimuli, which requires an integration of the various lines forming the object.

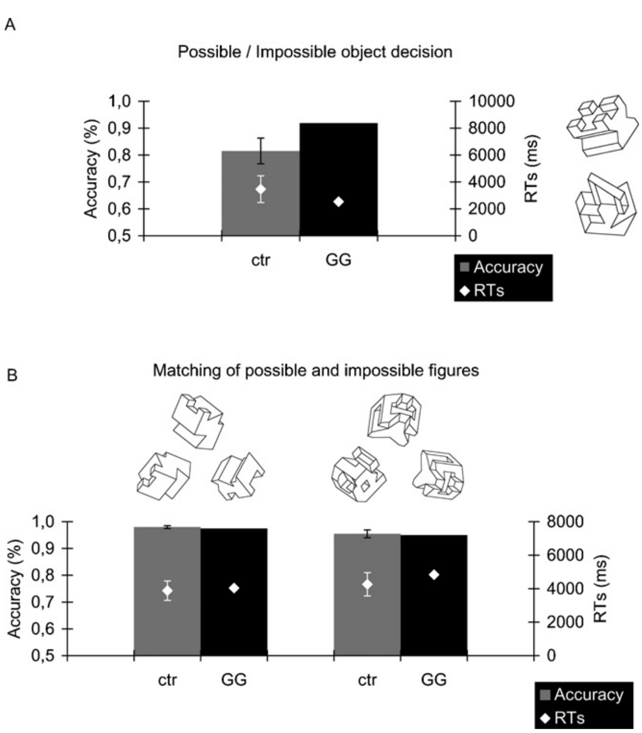

Fig. 10. Results of GG and age-matched controls in experiments 10–12: perception of 3D figures. (A) Results in the possible/impossible object decision task. (B) Results in the matching of possible and impossible figures tasks. Bars represent standard errors.

3.3.3. *Experiment 13. Discrimination of dot configurations*

Rationale. The purpose of this task was also to assess the ability to perceive stimulus differences defined in terms of their global organization or configuration. It was inspired from the work of Barton et al., 2004 who showed that a number of cases of acquired prosopagnosia were unable to perceive global patterns of dots. The authors used configurations of four gray dots in which they changed the horizontal position, the vertical position, or the brightness. They showed that four out of five prosopagnosic patients (004,

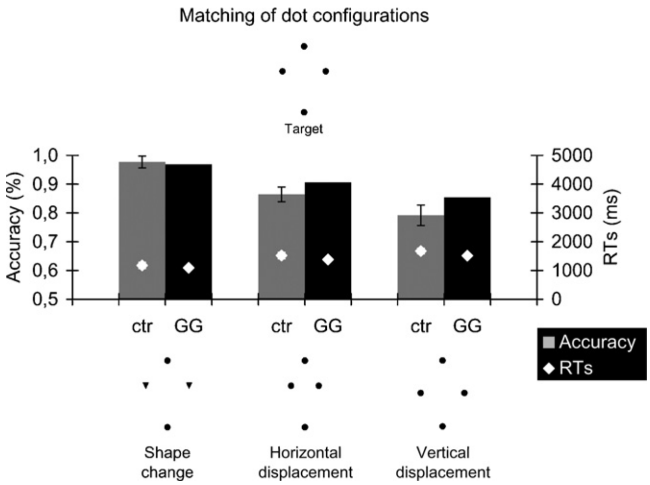

Fig. 11. Results of GG and age-matched controls in experiment 13: matching of dot configurations. Bars represent standard errors.

005, 006 and 007) were impaired in detecting vertical and horizontal changes in the four-dots configuration. Another task using configurations of two, four and eight dots (Barton, 2008b; Barton et al., 2004), showed that three other prosopagnosic patients (009, 010 and 015) had difficulties with these kinds of stimuli. However, once again, all the patients who failed a dots configuration task presented large low-level visual defects and/or clear visual agnosia. An exception is 009 (Barton et al., 2004) who presented with a more face-specific disorder, but who also was less impaired that the other patients tested with the configurations of two, four and eight dots. Barton (2009) replicated the findings of dots pattern processing impairment in the same patients (004, 005, 006 and 007)

Material and procedure. We created 24 stimuli corresponding to 24 different configurations of four dots (Fig. 11). Each stimulus was modified at three levels: (1) two dots were displaced vertically (upper or lower displacement of 45 pixels for each dot); (2) two dots were displaced horizontally (closer or further displacement of 45 pixels for each dot); (3) two dots were changed featurally (rings were exchanged with triangles). Thus we obtained three conditions referred to as: “vertical displacement”, “horizontal displacement” and “shape change” (Fig. 11). The task was a delayed two-alternative forced choice matching. A first configuration of dots appeared at the screen during 2000 ms. This target was followed by a mask (monochromatic Gaussian noise) of 500 ms and an ISI of 600 ms. Then, two probes appeared, one of them being the target, the other one being one of the three changed configurations. The participant had to answer by indicating whether the left or right probe stimulus corresponded to the target. Each stimulus was presented with its six modifications, as the target and as the distractor, leading to 288 trials (96 per condition). The experiment was divided into four blocks of 72 randomized trials. Randomization was important, so that the observers did not know, at the time of encoding, which aspect of the stimulus was diagnostic for the trial (i.e. how the target and distractor would differ). Hence, the participants were forced to encode all possible diagnostic aspects of the stimuli, including one possible local shape and two possible metric distances, changing the overall configuration of the dot pattern. The stimuli subtended 8.5° in height and 6.4° in width, on a white background.

Control participants. Five healthy males were tested (mean age: 66; SD: 2.83).

Results. Unsurprisingly, control participants found it easier to detect the *shape change* modification relative to the modifications requiring integrating information about several dots (Fig. 11). Once again, the performance of GG in this experiment was completely normal, quantitatively and qualitatively (i.e. showing the same pattern of performance as normal controls). His accuracy rate was in the normal range for the three types of modifications: *shape change* (GG: 96.9%; mean: 97.7%, SD: 4.56; $t = 0.166$, $p = 0.44$), *horizontal displacement* (GG: 90.6%; mean: 86.5%, SD: 5.75; $t = 0.662$, $p = 0.27$), and *vertical displacement* (GG: 85.4%; mean: 79.2%, SD: 7.93; $t = 0.719$, $p = 0.26$). His correct response times were also in the same range as the controls: *shape change* (GG: 1096 ms; mean: 1178 ms, SD: 251; $t = 0.298$, $p = 0.39$), *horizontal displacement* (GG: 1381 ms; mean: 1518 ms, SD: 252; $t = 0.496$, $p = 0.32$), and *vertical displacement* (GG: 1513 ms; mean: 1676 ms, SD: 223; $t = 0.667$, $p = 0.27$) (Fig. 11). This experiment further indicates that GG is able to process relative distance modifications of dot configurations and brings further evidence supporting his intact general integrative abilities.

3.3.4. Experiment 14. Processing of relative distances in non-face object: butterflies

Rationale. This task was also conducted to assess the ability to discriminate stimulus that differed in terms of their global configuration. The interest of this task is that we manipulated this time the global organization of a real non-face object, and that the category used was a living object, namely butterflies. Vertical and horizontal distances were manipulated and the task was proposed in two conditions in which the participant is aware or not of the location of the (diagnostic) changes on the stimuli. This kind of experiment has been tested previously with face stimuli in prosopagnosic patients (e.g., Barton, 2008a; Barton et al., 2002; Bukach et al., 2008; Joubert et al., 2003; Ramon & Rossion, 2010) but never, to our knowledge, with non-face (living) stimuli

Material and procedure. We selected eight pictures of butterflies on the web, half of them being assigned for one of the two types of modifications (vertical and horizontal). For the four first butterflies, the vertical position of two marks was symmetrically modified (Fig. 12A). We applied five degrees of translation: 10, 20, 30, 40 and 50 pixels. The other four butterflies were modified horizontally, the distance between two marks being modified according to five degrees: 10, 20, 30, 40 and 50 pixels. In each trial of the experiment, three stimuli appeared simultaneously on the screen, vertically shifted back: two pictures of the original butterfly and one of the five modified versions of this butterfly (Fig. 12A). The task was to indicate which butterfly was different from the other two. Participants were asked to answer by pressing a key corresponding to the position of the butterfly at the screen (1 for the one at the left; 2 for the one in the middle; 3 for the one at the right). There was no time constraint to respond. The experiment was divided into two blocks of 20 random trials (one block contained the stimuli vertically modified and the other the stimuli horizontally modified), and two trials were presented as examples first (not analyzed). The experiment was run twice, with two different instructions. In the first part – “Global condition” – participants were asked to choose which picture was different from the two others. In the second part – “Focus condition” – participants were informed that *certain marks* were displaced and that they had to choose the stimulus in which the marks were not at the same place. The stimuli subtended 8.5° in height and 11.3° in width, on a white background.

Control participants. Eight healthy males were tested (mean age: 59.4; SD: 4.53).

Results. This time again GG obtained a normal performance to detect changes in terms of displacement of features. First, in the “Global condition”, GG was as accurate as the age-matched controls, for the vertical displacements (GG: 90%; mean: 89.38%, SD: 9.8; $t = 0.060$, $p = 0.48$) and for the horizontal displacements (GG: 90%; mean: 87.5%, SD: 14.14; $t = 0.167$, $p = 0.44$) (Fig. 12B). All participants were relatively slow, reflecting presumably the difficulty of the task when they do not know how stimuli differ, and consider-

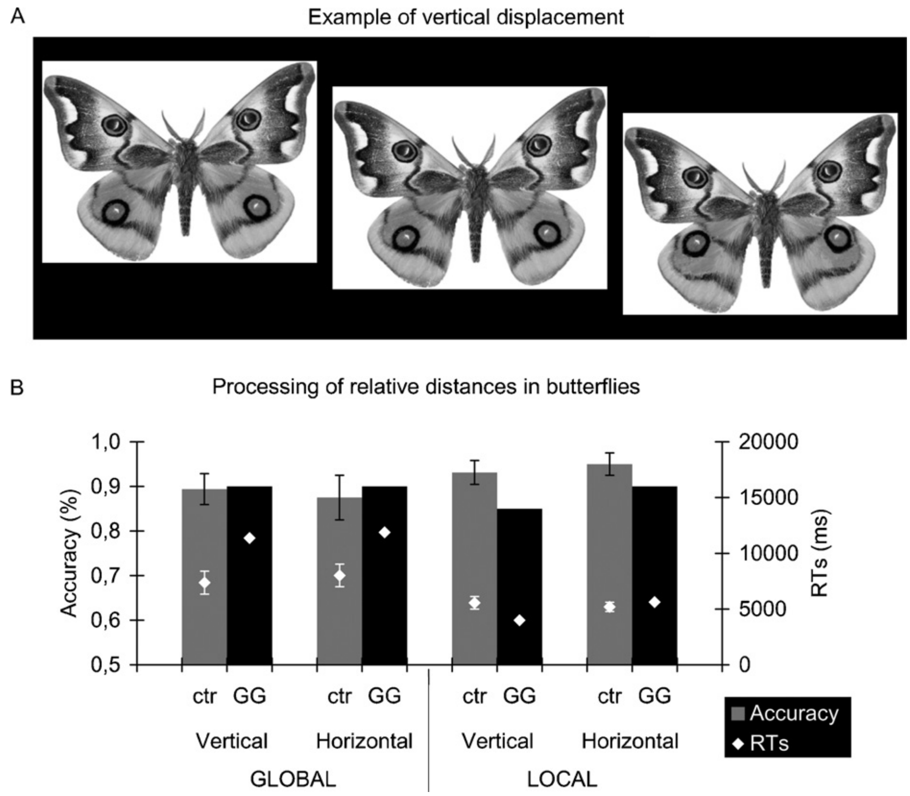

Fig. 12. (A) Example of trial used in experiment 14: processing of relative distances in butterflies. (B) Results of GG and age-matched controls in the task of processing relative distances in butterflies. Bars represent standard errors.

ing that there was no time constraint. GG's RTs were in the normal range, both for the vertical displacements (GG: 11362 ms; mean: 7377 ms, SD: 2910; $t = 1.291$, $p = 0.12$) and the horizontal displacements (GG: 11891 ms; mean: 8018 ms, SD: 2882; $t = 1.267$, $p = 0.12$) (Fig. 12B).

Second, in the "Focus condition", GG also obtained normal accuracy rates for the two types of modifications (Vertical: GG: 85%; mean: 93.13%, SD: 7.53; $t = 1.018$, $p = 0.17$; Horizontal: GG: 90%; mean: 95%, SD: 7.07; $t = 0.667$, $p = 0.26$) and was as fast as the controls (Vertical: GG: 3992 ms; mean: 5562 ms, SD: 1599; $t = 0.926$, $p = 0.19$; Horizontal: GG: 5620 ms; mean: 5194 ms, SD: 1168; $t = 0.344$, $p = 0.37$) (Fig. 12B).

This experiment brings further evidence that GG is able to process relative distances between features when embedded in living objects other than faces. More importantly, GG succeeded even when he did not know what type of change was applied. Together with the previous observations, this result indicates that GG shows preserved abilities in processing fine metric changes in non-face objects, which require to consider several elements of the object, not only a local part.

Altogether, the six experiments of this section bring strong evidence that GG's impairment is specifically restricted to faces. A systematic and comprehensive investigation of visual object processing indicates that GG has preserved abilities in integrating local parts and relations in global shapes and configurations. Furthermore, when having to discriminate individual items of a nonface category using distances between parts, he performs in the normal range. Importantly, this last result should not be taken as evidence that he shows normal abilities to process individual items of a nonface category holistically. Rather, it is likely that normal observers, when having to perform this task, do not rely naturally on holistic processes, but on a non-expert analysis of relative distances between two elements, which is time-consuming. Despite his low-level visual impairment (left hemianopia), GG did not show any difficulties for this type of task.

Nevertheless, despite these preserved abilities, GG is strongly impaired at processing faces, as demonstrated in the first section of this paper. If GG's prosopagnosia cannot be explained by a general impairment in Gestalt/holistic processing of complex objects, what is the nature of his disorder? Either the cause of GG's prosopagnosia is not related to a holistic processing impairment, or this holistic processing impairment is specific for faces. If this is the case, we should obtain evidence that holistic processing can be functionally dissociated between objects and faces.

To test this hypothesis, we proceeded in two steps. First, we tested holistic perception in *face detection*, that is, telling whether a visual stimulus is a face or not. Second, we assessed holistic perception in individual *face recognition/discrimination*. We hypothesized that detection of faces based on holistic processing would be preserved for GG – just as basic-level object recognition is preserved – while holistic processing of individual faces would be impaired.

3.4. Basic-level face categorization or face detection: experiments 15–17

In this fourth section, we aimed to assess the abilities of GG to perceive a stimulus as a face when it requires integrating features into a configuration rather than using specific elements. Obviously, this requires first to ensure that the patient is able to classify a stimulus as a face (face detection). Classically, acquired prosopagnosic patients are reported as being unimpaired at classifying a visual stimulus as a face, a process referred to as "face detection" or "basic-level face categorization" (Bobes et al., 2003; Bruyer et al., 1983; De Haan et al., 1987; Etcoff, Freeman, & Cave, 1991; Steeves et al., 2006; Young et al., 1990). These patients were tested in tasks of face/no-face decision in which the distractors were either jum-

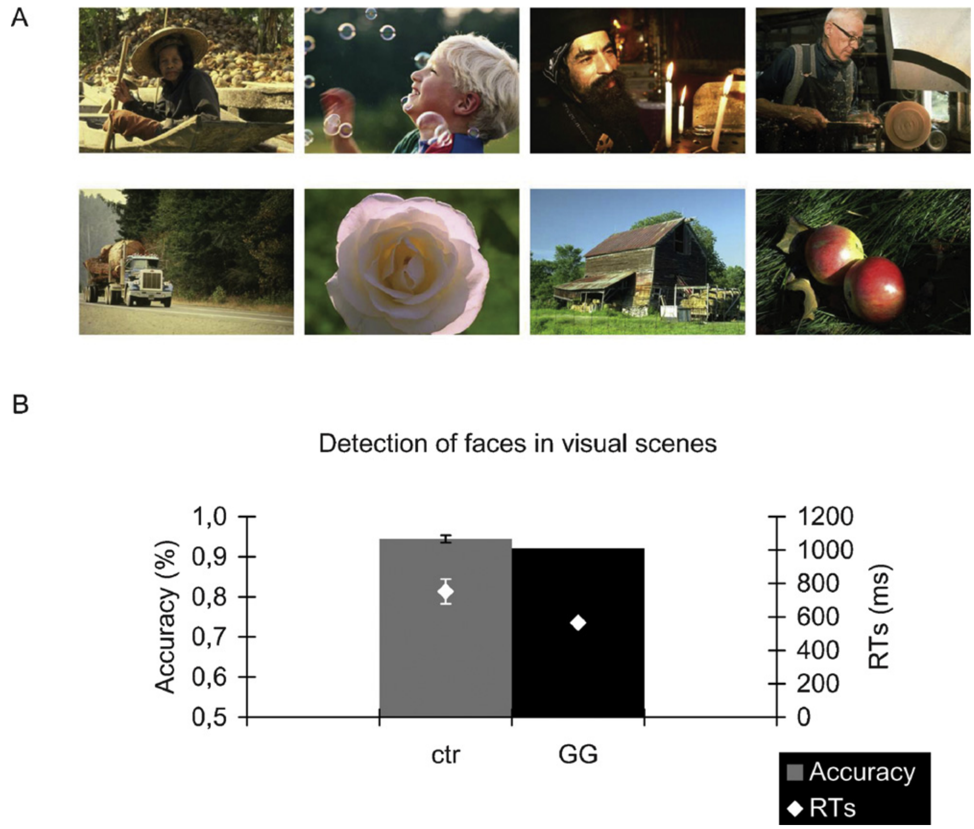

Fig. 13. (A) Example of face and nonface stimuli used in experiment 15: detection of faces in visual scenes. (B) Results of GG and age-matched controls in the task of detecting faces in visual scenes. Bar represents standard error.

bled faces (Davidoff & Landis, 1990; De Haan et al., 1987; Etcoff et al., 1991) or other categories of objects such as dogs, cars, housefronts (Bobes et al., 2003; Bruyer et al., 1983; Steeves et al., 2006; Young et al., 1990). All the patients tested with this kind of task show normal performance. However, there is in fact little empirical evidence that these patients are truly unimpaired at detecting/categorizing a visual stimulus as a face in more demanding situations. Here, based on the outcome of experiment 5, in which the participants had to discriminate a face from another visual category in one of the conditions, it may be hypothesized that GG has a completely preserved ability to categorize a stimulus as a face. Yet, face detection can be much more challenging if the visual stimulus is not segmented from the background for instance. Our first experiment aimed at testing face detection for stimuli embedded in visual scenes.

3.4.1. Experiment 15. Detection of faces in visual scenes

Rationale. This basic investigation required the detection of faces in natural visual scenes. During this task, GG and control participants were presented with full-screen pictures in which he had to decide as accurately and rapidly as possible if a face was present or not.

Material and procedure. The visual scenes were full color pictures of natural scenes found on the web, with a large sample identical to natural scenes used in face detection tasks in previous studies (e.g., Rousselet, Macé, & Fabre-Thorpe, 2003). We selected 100 non-face pictures (landscapes, vegetables and vehicles) and 100 face stimuli (real life scenes in which a face is present). Faces vary tremendously in size, orientation, location on the scene, presence of the body or not, and are presented under various backgrounds, so that the task cannot be done by simply attending a few elements at the same location. They also differ in terms of internal facial aspects, such as expression, age, gender and race (Fig. 13A). Pictures were presented one-by-one very rapidly. Each trial began with a fixation cross (300 ms) and an ISI (300 ms) and was followed by the target presented very quickly during 50 ms (unmasked). A white screen followed, and the participant had to decide if he saw a face or not in the visual scene, by pressing a corresponding key. The experiment was divided into two blocks of 100 randomized trials. The stimuli were projected in full-screen size.

Control participants. Five healthy males were tested (mean age: 66; SD: 2.83).

Results. In spite of his left hemianopsia and the very fast presentation, GG succeeded very well in this experiment. His accuracy was as high as controls (GG: 92.1%; mean: 94.4%, SD: 2.02; $t = 1.067$, $p = 0.17$) and he was at least equally fast (GG: 566 ms; mean: 752 ms, SD: 166; $t = 1.023$, $p = 0.18$) (Fig. 13B). Based on these first observations, one can safely argue that in normal viewing conditions, categorizing a visual stimulus as a face is an easy task for prosopagnosic patient GG, this despite his left hemianopia.

3.4.2. Experiment 16. Mooney faces

Rationale. In all examples above, and in most real life circumstances, categorizing a visual stimulus as a face can be done by identifying a contour that can easily be segmented from the background, or a few clear elementary facial features (and particularly the eyes; e.g., Lewis & Edmonds, 2003). However, a visual stimulus can be also readily categorized as a face even if it does *not* contain clear elementary facial features, its faceness being defined solely or primarily by the global organization of the elements. A classical example is provided by two-tone (thresholded, black and white) images of faces introduced in the 1950s (Mooney, 1956; Mooney, 1957) to test the ability of children to form a coherent percept of shape on the basis of very little detail. These "Mooney" faces (Fig. 14) have been of great interest to psychologists and neu-

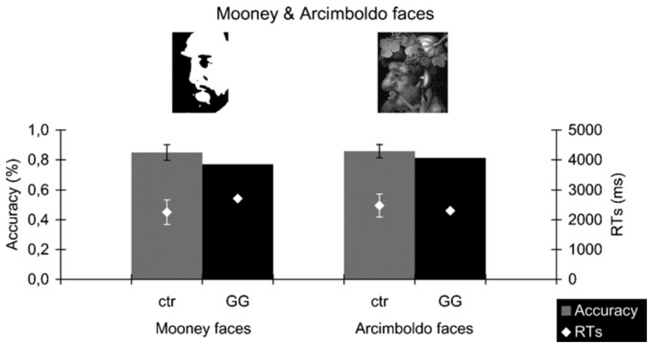

Fig. 14. Results of GG and age-matched controls in experiments 16 and 17: detection of Mooney and Arcimboldo faces. Bars represent standard errors.

roscientists throughout the past half a century (e.g., George, Jemel, Fiori, & Renault, 1997; Jeffreys, 1989; McKone, 2004; Mooney, 1956, 1957; Moore & Cavanagh, 1998; Parkin & Williamson, 1987; Perrett et al., 1984) because of their ambiguous nature, specificity (two-tone faces seem more readily identifiable than other objects; Moore & Cavanagh, 1998) and their sudden interpretability. In a Mooney image, the local features often become too ambiguous to be recognized individually, and must be disambiguated based on their context within a global configuration, a process that appears to depend on internal 2D face representations (Cavanagh, 1991; Hegdé, Thompson, & Kersten, 2007; Kemelmacher-Shlizerman, Basri, & Nadler, 2008; Moore & Cavanagh, 1998). Indeed, when a Mooney picture is presented upside-down, the face is usually not perceived (Fig. 14), presumably because the visual input cannot be disambiguated with the help of internal 2D global representations (Cavanagh, 1991). It is with photographs of faces that these observations are most spectacular (Moore & Cavanagh, 1998). Although many other cases of acquired prosopagnosia have been tested with Mooney face stimuli, most of these tests were part of a clinical neuropsychological preliminary report (a test of visual closure) rather than a systematic experiment. The classical test of Mooney (1957) consists in 40 items that have to be sorted in six categories (girl, boy, grown-up woman, grown-up man, old woman, old man).

Many patients have been reported to be impaired at Mooney face perception (PH, De Haan et al., 1987; KD, RB and AH, Davidoff & Landis, 1990; SP, Young et al., 1990; RM, PM and PC, Sergent & Signoret, 1992a), but some were also reported to perform in the normal range (BM, Sergent & Villemure, 1989; PV, Sergent & Poncet, 1990; DC, Rivest et al., 2009). However, these investigations were never systematic. Specifically, the patient data was rarely compared to appropriate control data, the patients were tested in variants of face/non face decision task (i.e. categorizing the Mooney faces according to gender and age), and response times were rarely considered [excepted in the case of PV (Sergent & Poncet, 1990) who showed normal speed]. A more in depth investigation of Mooney stimuli in prosopagnosia was conducted recently with the patient DF (Steeves et al., 2006). The authors tested the patient in two tasks (Mooney face/non-face discrimination and upright/inverted Mooney face discrimination) and they compared her results with a group of age-matched controls. DF, who is visual agnosic (Milner et al., 1991), was impaired in both accuracy and latency in the two tasks. Most recently, we examined extensively the patient PS with Mooney stimuli in a behavioural and neuroimaging study (Rossion, Dricot, Goebel, & Busigny, submitted). Contrary to the patient DF, PS's processing of the Mooney faces is behaviourally completely normal.

Material and procedure. The stimuli were selected from the dataset originally created by Schurger and colleagues (Art of Science Competition, Princeton University, http://www.princeton.edu/artofscience/gallery). This type of stimuli was created following the same procedure that the one used by Mooney (1956, 1957) in his study to explore the perceptual closure ability – that is the ability to form a global and coherent perceptual representation on the basis of few details. Eighty Mooney faces among the Schurger's set were selected (Fig. 14). These 80 selected items were presented upright and upside-down, and were displayed in random order in two blocks of 80 trials. Each picture appeared on the screen one after the other, and the observers had to decide whether they could see a face in the stimulus or not by pressing a corresponding key. For the Mooney pictures presented in the upright orientation (80 trials), the response expected was "face", for the Mooney pictures presented in the inverted orientation (80 trials), the response expected was "no face". The stimuli were presented on the screen until the response of the participant, and were followed by a central cross (300 ms) and a gray screen (300 ms). The stimuli subtended approximately 5.4° in height and 3.8° in width and were presented on a gray background (128, 128, 128).

Control participants. Five healthy males were tested (mean age: 66; SD: 2.83).

Results and discussion. GG's accuracy was not different from that of control participants (GG: 76.9%; mean: 84.9%, SD: 11.75; $t = 0.622$, $p = 0.28$) and he was as fast as controls (GG: 2712 ms; mean: 2255 ms, SD: 924; $t = 0.451$, $p = 0.34$) (Fig. 14).

These results, along with converging evidence from the recent report of normal face detection in Mooney stimuli by the patient PS (Rossion et al., submitted), provide evidence that severe acquired prosopagnosia does not necessarily prevent the accurate and rapid categorization of a visual stimulus as a face, even when the stimulus cannot be readily identified as a face based on local elements. Obviously, one would not expect all acquired prosopagnosic patients to be intact at this task, in particular if a global integrative form processing impairment affects shapes grouping, as was the case with the patient DF for instance (see a previous description of the patient in e.g., Milner et al., 1991).

3.4.3. Experiment 17. Arcimboldo faces

Rationale. Another challenging face detection/basic-level categorization can be proposed to prosopagnosic patients by confronting them to face stimuli made of non-facial elements. The best known examples are the famous paintings of Giuseppe Arcimboldo (16th century; Hulten, 1987), in which a face is constituted of nonface (usually organic) elements such as fruits and vegetables, animals, flowers (Fig. 14). Here, the elements can be identified relatively easily, but they correspond to nonface objects rather than to elementary facial features. Like Mooney stimuli, an Arcimboldo painting can be categorized as a face due to the global face configuration formed by these non-face elements rather than the identification of the elements themselves. As a matter of fact, a visual agnosic patient who cannot identify the constituent object elements may still perceive the face in these Arcimboldo paintings (Moscovitch et al., 1997), indicating that the face is perceived independently of the nature of the elements *per se*. Again, the face is usually not perceived when the painting is presented upside-down, an aspect that was used by the artist Arcimboldo to make his paintings reversible (Fig. 14; Hulten, 1987). While it is a common belief that prosopagnosic patients are unable to see an Arcimboldo painting as a face (Harris & Aguirre, 2007), no evidence was provided in the literature that this kind of task was systematically failed in prosopagnosia. Steeves et al. (2006) showed that their visual agnosic patient, DF, was not able to describe paintings of Arcimboldo, but Rivest et al.'s (2009) patient DC could see the face in a few of them as well as normal controls. However, the first psychometric evaluation of face detection in prosopagnosia with Arcimboldo paintings was conducted with the patient PS (Rossion et al., submitted). The results showed that she was as accurate and fast as the controls, as she did in the Mooney task.

Material and procedure. The stimuli used here were inspired by the paintings of the 16th century artist, Giuseppe Arcimboldo (see Hulten, 1987; or for example http://www.artyst.net; 14 stimuli) and by the creations of the contemporary mosaic portrait artist, Jason Mecier (http://www.jasonmecier.com; 26 stimuli). Both of them created works of art consisting in faces composed by non facial elements (vegetables, fruits, animals, candies, stationeries, pebbles, . . .). The pictures were downloaded from the websites and were cropped so that only the area of the face was present. Next, the pictures were homogenized to have roughly the same size and resolution. In total, 40 color "Arcimboldo" face stimuli were created (Fig. 14). These 40 created items were presented at upright and upside-down orientation, and were displayed randomly in two blocks of forty trials. The procedure and the instructions were similar to the Mooney faces experiment. For the "Arcimboldo" pictures presented in the upright orientation (40 trials), the response expected was "face", for the "Arcimboldo" pictures presented in the inverted orientation (40 trials), the response expected was "no face". The stimuli subtended approximately 5.3° in height and 4.6° in width and were presented on a gray background (128, 128, 128).

Control participants. Five healthy males were tested (mean age: 66; SD: 2.83).

Results and discussion. Again, in this experiment, GG presented a profile of response that was not different from the control participants, both for accuracy and response times. He was very accurate (GG: 81.3%; mean: 85.8%, SD: 9.98; $t = 0.412$, $p = 0.35$) and fast (GG: 2303 ms; mean: 2481 ms, SD: 865; $t = 0.188$, $p = 0.43$) (Fig. 14).

These three experiments indicate clearly that the patient GG is perfectly able to categorize a visual stimulus as a face. He has no complaints in real life about this, and showed normal performance even in difficult circumstances. In this respect, he shows a comparable response profile to another case of acquired prosopagnosia, with a different etiology and localization of brain damage, the patient PS (Rossion et al., 2003).

Here, we demonstrated that the problem of the patient is not in classifying a stimulus as a face, even when it requires an analysis of the whole stimulus configuration rather than specific local elements. These observations are consistent with what we found for objects: the patient *is* able to perceive a global form, and even to extract local information (details) and take into account changes in terms of distances between these details (cfr. experiment 14).

Nevertheless, we have shown that GG has a massive prosopagnosia, showing great difficulties when having to individualize faces. In the next section, we proceeded to assessing the nature of his prosopagnosia by asking him to individualize faces in which we manipulated different kinds of information.

3.5. Recognition of individual faces: experiments 18–24

So far, we have demonstrated that GG presents with a recognition impairment restricted to individual faces. However, he has intact face detection/basic-level categorization, even when a form of global or holistic perception such as for Mooney or Arcimboldo-facelike stimuli is required. In this final set of tasks, we aimed at understanding more precisely what causes GG's difficulties in dealing with individual faces. In a first subsection, we evaluated the role of specific facial features and relations between them in tasks of individual face recognition (experiments 18 and 19). In the second subsection we assessed GG's abilities at processing individual faces holistically using well-known paradigms and effects: face inversion (experiments 20–22), whole-part face (experiment 23) and composite face effects (experiment 24).

3.5.1. Facial features and relations between them in individual face recognition

As briefly indicated in Section 1, there is recent evidence that acquired prosopagnosia can lead to a lack or reduced sensitivity to diagnostic information located in the eyes area of individual faces. Using a learning paradigm followed by an identification task of faces masked with random apertures ("Bubbles", Gosselin & Schyns, 2001), Caldara et al. (2005) tested the brain-damaged patient PS (Rossion et al., 2003). In contrast to normal viewers, who relied extensively on localized information on the eyes of the faces, PS needed much more information to achieve the same level of performance, and relied mostly on the mouth and lower contours of the faces rather than the eyes. Bukach et al. (2006) showed that the brain-damaged prosopagnosic patient LR was able to detect small shape changes in the mouth region as well as variations in metric distances between features of the lower area of the face (e.g., nose–mouth distance), but was strikingly impaired at making similar judgments on the eyes of faces. Most recently, Bukach et al. (2008) extended these observations on LR and another case of prosopagnosia (HH) using a *Face Dimensions Task* in which the participant's sensitivity to parametric manipulations to the shape and distance of facial features was tested. While the patients performed like control participants on all types of changes applied to the mouth, they were severely impaired for individual face discrimination based on the eyes. Similar observations in this experiment were made with the patient PS (Rossion et al., 2009), who has also been shown to fixate her gaze mainly to the mouth when identifying personally familiar faces (Orban de Xivry et al., 2008; Van Belle, de Graef, Verfaillie, Busigny, et al., 2010).

3.5.1.1. Experiment 18. Simultaneous discrimination task with preview. Material and procedure. The stimuli were those used in Goffaux and Rossion (2007). In the experiment, there were four randomly interleaved stimulus conditions (eyes featural, eyes vertical, eyes horizontal, and nose–mouth featural). As usual, face stimuli were free of facial hair, glasses and hairline in order to remove any external cue to face perception. The inner features of each face (eyes, nose and mouth in their original spatial relations) were pasted on a generic face shape. Then each stimulus underwent four kinds of modifications: (1) eyes-featural (contrast of eyes were made darker or lighter, with small modifications of shape), (2) eyes-vertical (eyes moved upward or downward in the face), (3) eyes-horizontal (smaller or larger inter-ocular distance), and (4) lower part of the face (nose and mouth were exchanged with those of another face) (see Goffaux & Rossion, 2007). The task was a simultaneous matching with a preview of the target. Trials began with the target face presented alone at the top of the screen. After 2000 ms, two probe stimuli located side by side below the target appeared on the screen and remained until a response. One of the probe stimuli was identical to the target and the distractor – for half of the trials on the left, randomly – was one of the four modified faces of this target-face. Participants had unlimited time to answer by indicating whether the left or right probe stimulus corresponded to the target. Twenty full-front gray scaled pictures of faces (half males) with a neutral expression were used. Each trial was repeated twice, leading to 40 trials per condition. The experiment was divided into two blocks of 80 randomized trials. The stimuli subtended approximately 9.2° in height and 7.1° in width, on a gray background.

Control participants. Five healthy males were tested (mean age: 67.7; SD: 2.31).

Results and discussion. Control participants performed the task very well for all conditions (Bottom: 92%, SD: 7.58; Eyes featural: 91.5%, SD: 8.77; Eyes horizontal: 97%, SD: 2.09; Eyes vertical: 98%, SD: 2.09) (Fig. 15), with no difference between the 4 conditions ($F_{(1,4)} = 1.471$, $p = 0.14$). They took on average around 3000 ms to

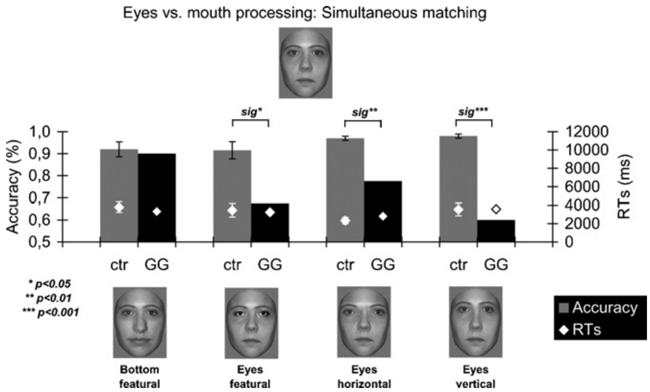

Fig. 15. Results of GG and age-matched controls in experiment 18: processing of facial features and relations between them in individual face recognition–simultaneous matching. Bars represent standard errors.

perform the task, with no significant difference between conditions ($F_{(1,4)} = 2.087$, $p = 0.08$). In contrast, GG was strongly impaired in the three conditions involving a modification at the level of the eyes (Eyes featural: 67.5%, $t = 2.498$, $p < 0.05$; Eyes horizontal: 77.5%, $t = 8.517$, $p < 0.01$; Eyes vertical: 60%, $t = 16.598$, $p < 0.001$). However, he performed in the normal range in the condition in which the bottom of the face was diagnostic (90%, $t = 0.241$, $p = 0.41$) (Fig. 15). In the four conditions, GG was as fast as the controls (Bottom: 3331 ms, $t = 0.331$, $p = 0.38$; Eyes featural: 3237 ms, $t = 0.118$, $p = 0.46$; Eyes horizontal: 2805 ms, $t = 0.529$, $p = 0.31$; Eyes vertical: 3582 ms, $t = 0.023$, $p = 0.49$) (Fig. 15).

In line with the hypothesis, these observations indicate that patient GG, who was not given any specific instruction to match the face and had unlimited time to respond, was able to use the diagnostic information at the level of the lower part of the face, in particular the mouth. Importantly, these results cannot be accounted for by an increased difficulty of the conditions involving the eyes of the face, as the controls performed equally well in all four conditions (see also Goffaux & Rossion, 2007). The most likely explanation is that the patient GG, like other cases of acquired prosopagnosia, spontaneously attended to the mouth area of the face and was able to perform the task when that information was diagnostic. Either he totally ignored the information at the level of the eyes, or he was unable to extract diagnostic information at this level. The second hypothesis is probably more likely, since GG scored above chance level in all conditions involving a modification at the level of the eyes, and also showed differences in performance between these conditions. Interestingly, he was most impaired in the condition involving a modification of the position of the eyes in the vertical direction (Fig. 15).

3.5.1.2. Experiment 19. Delayed discrimination task, eyes and mouth. Rationale. This experiment was previously described by Bukach et al. (2008) and Rossion et al. (2009) and was conducted here to strengthen and refine the observations above. One obvious interest of this last experiment is that it has been performed already with three cases of acquired prosopagnosia, showing consistent results. The other interest is that the diagnosticity of the face stimuli is limited to the eyes or the mouth (not the entire lower part of the stimulus as in the experiment above), and contains an equal amount of trials. Finally, since some authors have suggested that cases of prosopagnosia suffer from a particular impairment at processing relative distances between faces (and objects) (Barton, 2008a; Barton et al., 2002), the kind of manipulations used here offers a test of this hypothesis.

Material and procedure. The task consisted in a delayed same/different identity decision. The stimuli consist of grayscale digitized photographs of four male and four female faces. An original face was modified along four dimensions: relational/eyes, relational/mouth, featural/eyes, and featural/mouth. Each dimension consisted of five faces, the original face and four modified face images. The modified faces in the *relational/eyes dimension* were created by moving each eye closer together on the horizontal axis by 5 pixels or 10 pixels (conditions 1 and 2); or moving each eye farther apart by 5, 10 pixels (3 and 4) – always relative to the original face. The modified faces in the *relational/mouth dimension* were created by moving the mouth on the vertical axis closer to the nose by 5, 10 pixels or moving the mouth away from the nose by 5, 10 pixels. The modified faces in the *featural/eye dimension* were created by increasing the size of the eyes by 10%, 20% or decreasing the size of the eyes by 10%, 20%. The modified faces in the *featural/mouth dimension* were created by increasing the size of the mouth by 10%, 20% or decreasing the size of the mouth by 10%, 20%. Eight original faces (four male, four female) were used as stimuli. In total there were 136 face images: eight face sets each consisting of an original face and four modified faces within the four dimensions. For each trial, a fixation cross was presented for 150 ms, followed by a study face that appeared for 500 ms, and then after an interstimulus interval of 500 ms, the second test face appeared. If the test face was perceived to be identical to the study face, participants were instructed to press the key labeled “same”; otherwise, they were to press the key labeled “different”. The study face remained in view until participants indicated their response with a key press. Participants were given a maximum of 3000 ms to respond. The experiment consisted of a total of 512 trials presented randomly. For half the trials the two images were identical and for half the trials the images were different. There were an equal number of trials from the eight faces, the four dimensions (relational/eyes; relational/mouth; featural/eyes; featural/mouth) and four degrees of difference within each dimension. Each same and different condition was repeated twice. All stimuli subtended approximately $5.72^{\circ} \times 8.10^{\circ}$. Since this task was not a forced choice procedure, the data was analyzed by computing the d' scores for each participant, taking into account both the hits and false alarms in the measure of performance.

Control participants. Six healthy males were tested (mean age: 63.3; SD: 5.5).*Results and discussion*. Control participants obtained high d' sensitivity scores for all conditions (Relational-Eyes: $d' = 1.43$, SD: 0.41; Relational-Mouth: $d' = 1.82$, SD: 0.34; Featural-Eyes: $d' = 1.48$, SD: 0.24; Featural-Mouth: $d' = 1.73$, SD: 0.64) (Fig. 16A), with no difference between the 4 dimensions ($F_{(1,5)} = 1.187$, $p = 0.17$). The control participants obtained the same profile with RTs on correct trials (Relational-Eyes: 1442 ms, SD: 248; Relational-Mouth: 1604 ms, SD: 604; Featural-Eyes: 1681 ms, SD: 692; Featural-Mouth: 1397 ms, SD: 526) (Fig. 16B), with no difference between the 4 dimensions ($F_{(1,5)} = 0.363$, $p = 0.39$).

In contrast, considering the d' sensitivity, GG was significantly impaired for the two conditions involving a modification at the level of the eyes (Relational-Eyes: $d' = 0.5$, $t = 2.093$, $p < 0.05$; Featural-Eyes: $d' = 0.63$, $t = 3.273$, $p < 0.05$) (Fig. 16A). However, he performed in the normal range in the conditions involving a modification at the level of the mouth, although he was slightly less efficient in the relational modification (Relational-Mouth: $d' = 1.22$, $t = 1.655$, $p = 0.08$; Featural-Mouth: $d' = 1.44$, $t = 0.429$, $p = 0.34$) (Fig. 16A). In the four conditions, GG was as fast as the controls (Relational-Eyes: 1265 ms, $t = 0.661$, $p = 0.27$; Relational-Mouth: 992 ms, $t = 0.938$, $p = 0.20$; Featural-Eyes: 1183ms, $t = 0.666$, $p = 0.27$; Featural-Mouth: 1048 ms, $t = 0.614$, $p = 0.28$) (Fig. 16B).

In summary, the results of GG in the present experiment are similar to the results reported for acquired prosopagnosic patients LR and PS [respectively described by Bukach et al. (2008) and Rossion et al. (2009)]. The results demonstrate that GG was impaired in his ability to detect relative distances between features as well as local

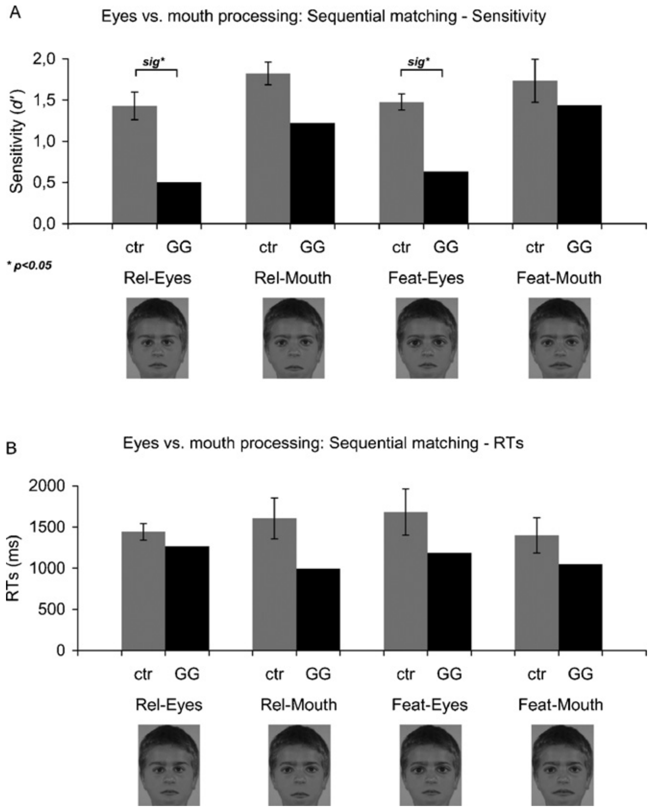

Fig. 16. Results of GG and age-matched controls in experiment 19: processing of facial features and relations between them in individual face recognition–sequential matching. (A) Sensitivity measures. (B) Correct response times. Bars represent standard errors.

featural differences in the eyes region of the face. However, he performed in the normal range for discrimination in the mouth region, although being less efficient to discriminate faces based on mouth height. These observations confirm a reduced sensitivity to the eyes region and a processing bias for the mouth.

In these two experiments, we demonstrated that GG had difficulties to process a specific region of the face (i.e. the eyes), and there were indications of even increased difficulties in conditions that particularly required integrating multiple features of the face (vertical displacements of the eyes in experiment 18, see Goffaux & Rossion, 2007; Sekunova & Barton, 2008; and of the mouth in experiment 19, see Rossion et al., 2009). However, GG's results do not provide us with much information about the nature of his prosopagnosia. It may be considered that difficulties in processing information around the eyes region may result from an impaired ability to integrate simultaneously the multiple information provided by this region of a face (e.g., pupils, eyelids, iris, eyebrows, distance between eyes, distance from nose and forehead) into a single representation (Caldara et al., 2005; Orban de Xivry et al., 2008). Indeed, impairment in holistic processing of the individual face may represent a solid hypothesis in order to explain the nature of GG's prosopagnosia. This hypothesis will be tested in the next section.

3.5.2. *Facial features and relations between them*

In the face processing literature, the term "holistic" has been widely used. In line with early (Galton, 1883) and more recent (e.g., Farah, Wilson, Drain, & Tanaka, 1998; Ingvalson & Wenger, 2005) proposals, "holistic face processing" could be defined as the *simultaneous integration of the multiple features and relations of an individual face into a global and single perceptual representation* (see Rossion, 2008a, 2009).

The view of impaired individual face holistic processing in prosopagnosia has been supported with different paradigms testing the inter-dependence between facial features (e.g., Boutsen & Humphreys, 2002; Saumier et al., 2001; Sergent & Villemure, 1989). Among these paradigms, some authors have used *multidimensional scaling of dissimilarity judgments* (Sergent & Poncet, 1990; Sergent & Signoret, 1992a; Sergent & Villemure, 1989), tasks of *whole-part superiority* (Boutsen & Humphreys, 2002; Davidoff & Landis, 1990; Delvenne et al., 2004; Ramon et al., 2010; Wilkinson et al., 2009), or tasks measuring *priming effect* of part and holistic information (Saumier et al., 2001). A number of studies have also concluded to a deficit of holistic face processing in prosopagnosia from an abnormal *effect of face inversion* (e.g., Boutsen & Humphreys, 2002; Delvenne et al., 2004; McNeil & Warrington, 1991; for a recent review, see Busigny & Rossion, 2010), which is actually an indirect evidence (see below).

All of these studies have provided partial evidence in support of the view that acquired prosopagnosia is characterized by a particular lack of ability to integrate features of the face into a global (i.e. holistic) representation. However, the use of different paradigms and the variability among the patients tested has hindered our understanding of the nature of this holistic processing impairment in acquired prosopagnosia.

In this study, we tested GG with three classical paradigms to assess holistic face processing: the face inversion effect, the whole-part face effect and the composite face effect.

3.5.2.1. *Face inversion effect.*

Inversion is perhaps the most widely used transformation that has been applied to face stimuli in the literature, following the work of Yin (1969), in which it was found that this manipulation affected much more the recognition of faces 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 (for recent reviews, see Rossion, 2008a, 2009), the vast majority of authors agree that inversion affects our ability to see a face holistically (Farah et al., 1998; Maurer, Le Grand, & Mondloch, 2002; Rossion, 2008a, 2009). Several cases of prosopagnosia have been tested with upright and inverted faces (e.g., Anaki et al., 2007; Barton, Zhao, & Keenan, 2003; Behrmann et al., 2005; Farah, Wilson, et al., 1995; Marotta et al., 2002; McNeil & Warrington, 1991; Riddoch et al., 2008; Rivest et al., 2009; Wilkinson et al., 2009; for a review see Busigny & Rossion, 2010). In a recent review of the effect of face inversion on prosopagnosia, we have argued that the inversion effect is abnormal in cases of prosopagnosia, being generally reduced or even abolished (Busigny & Rossion, 2010). However, the claim that it could be reversed (patients performing better with inverted faces, e.g., Farah, Wilson, et al., 1995) seems to reflect the exception rather than the rule and such effects probably reflect more the addition of a low-level visual impairment (i.e. upper visual field defect) to the prosopagnosia (see Busigny & Rossion, 2010).

3.5.2.2. *Experiment 20. BFRT upright and upside-down. Material and procedure.*

This first experiment is the administration of the classical BFRT (Benton et al., 1983). GG performed the BFRT for the first time shortly after his accident as part of his neuropsychological assessment, and obtained a score of 37/54. In the context of the present study, GG was administered with the BFRT once again, but this time upright and inverted. The first test was in the upright orientation (17/01/2007), and the second test in the inverted orientation (28/08/2007). The control participants performed the upright orientation first, like GG, but for practical reasons they carried out the inverted orientation one day later. If anything, when compared to GG, they should benefit more from the experience with upright faces when performing the test in an inverted orientation, reduc-

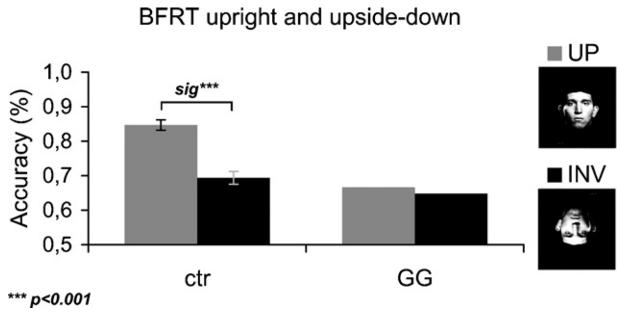

Fig. 17. Results of GG and age-matched controls in experiment 20: BFRT upright and upside-down. Bar represents standard error.

ing the size of their face inversion effect. This runs counter to our hypothesis or an abnormal (reduced or abolished) inversion effect for the patient GG relative to control participants.

Control participants. Eleven healthy controls were tested (8 females; mean age: 57.55; SD: 7.7).

Results. Analyses of average accuracy rates (paired sample *t*-test) revealed a massive face inversion effect for the control participants: 84.7% (SD: 6.09) for upright faces and 69.4% (SD: 4.92) for the inverted orientation ($t_{10} = 8.94$, $p < 0.001$). In contrast, GG obtained a significantly lower score in the upright condition in comparison to the control participants (66.7%, $t = 2.831$, $p < 0.01$), but he performed in the normal range for the inverted condition (64.8%, $t = 0.885$, $p = 0.20$). Importantly, GG did not present any difference between the upright and the inverted orientation ($t_{21} = 0.224$, $p = 0.41$) (Fig. 17). As expected, GG's score with inverted faces was virtually identical as for upright faces, to the point that it did not longer differed from that of normal participants for inverted faces. We also note that GG's score was clearly above chance level (18/54, =33%) in the BFRT test so that his absence of inversion effect could not be attributed to a floor effect.

Concerning RTs, the controls performed the test faster in the upright (mean: 5min51; SD: 77) than in the inverted orientation (mean: 7min42, SD: 141, $t_{10} = 3.56$, $p < 0.01$). Compared to controls, GG was not slowed down in both orientations (respectively 7min19, $t = 1.09$, $p = 0.15$; and 9min38, $t = 0.79$, $p = 0.23$). GG also appeared to be faster in the upright condition (no statistics could be performed here since only the total time to perform the test was calculated for both orientations, including the errors). In the next experiments, the RTs are calculated for correct responses, in order to investigate the presence or not of an inversion effect for the patient, thus considering speed as well as accuracy.

3.5.2.3. Experiment 21. Discrimination of upright and inverted faces. Material and procedure. The goal of this experiment was to replicate the observation of lack of face inversion effect with face photographs presented on a computer measuring RTs for each trial. The procedure used here was a delayed two-alternative force choice matching task. Sixteen color faces (8 females) were used, with two sets of photographs for each face (target and probe stimuli were always two different full front photographs of the same person). Each photograph was placed in an oval in order to remove the external cues (hair, ears, accessories, . . .) (Fig. 18). Each trial began with a white screen (1000 ms), followed by the target (3000 ms), an ISI (2000 ms), and the probe screen (infinite). Each new trial was initiated after the response of the participant. The participants were instructed to select one of the two faces that was the same as the previously shown target, by pressing a keyboard key (left or right) corresponding to the location of the target face. They were asked to be as accurate as possible, and respond as fast as they could. The 32 photographs were used two times in both orientations. The experiment was divided into two blocks of 64 randomized trials and a set of seven trials was presented as examples first (not analyzed). In total, 64 trials were used for both orientations. Stimuli subtended approximately 9.2° in height and 7.1° in width, on a white background.

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

Results. Control participants performed much better for upright than inverted faces [95.3% (SD: 3.63) *vs*. 88.4% (SD: 3.98); $t_{10} = 4.52$, $p < 0.001$]. In comparison to normal controls, GG was impaired for upright (88.3%, $t = 1.854$, $p < 0.05$) but not for inverted faces (88.3%, $t = 0.017$, $p = 0.49$). Most importantly, he did not present any inversion effect ($t_{254} = 0$, $p = 0.5$) (Fig. 18A).

Control participants showed also a strong face inversion effect in correct RTs [respectively 1562 ms (SD: 641) and 1984 ms (SD: 540) for upright and inverted faces; $t_{10} = 4.43$, $p < 0.001$]. GG was in the normal speed range for correct upright faces (1732 ms, $t = 0.254$, $p = 0.40$) and inverted faces (1613 ms, $t = 0.658$, $p = 0.26$). Although, statistically, the face inversion effect in RTs was almost significant

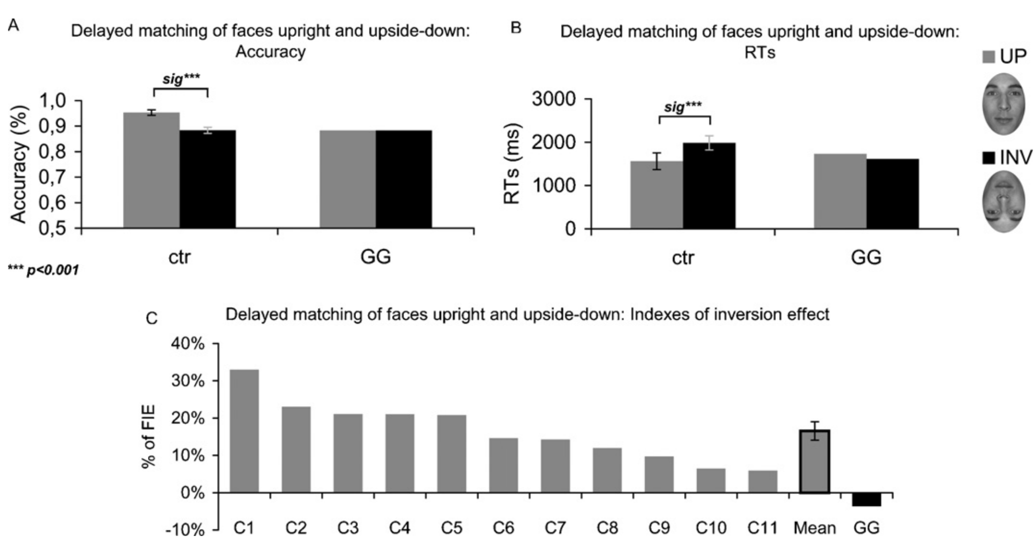

Fig. 18. Results of GG and age-matched controls in experiment 21: delayed matching of faces upright and upside-down. (A) Accuracy rates. (B) Correct response times. (C) Indexes of inversion effect calculated on inverse efficiency (RTs/accuracy) for each single participant. Bars represent standard errors.

(t_{214} = 1.60, p = 0.06), it was in fact opposite to that found in controls (Fig. 18B).

We also computed an index of inversion effect that combines the accuracy rates and correct RTs, in order to take into account possible speed–accuracy trade-offs and to assess the magnitude of the FIE for PS and each control participant. First, we computed the inverse efficiency (Townsend & Ashby, 1983). Next, we calculated the percentage of FIE for each participant using the following formula: (Inverse efficiency Upright − Inverse efficiency Inverted)/(Inverse efficiency Upright + Inverse efficiency Inverted). The results showed that GG had a significantly lower face inversion index (−3.57%) in comparison to the control participants (mean: 16.55%, SD: 8.14; t = 2.37, p < 0.05) (Fig. 18C). This experiment replicates the finding of the previous one with the BFRT, taking into account the response times for correct responses. Normal observers showed a strong face inversion effect both in accuracy and correct response times. In contrast, GG was impaired at the task only in upright condition, and he did not show any effect of face inversion, neither in accuracy rates nor correct RTs.

3.5.2.4. Experiment 22. Simultaneous matching of faces and cars upright and upside-down. Material and procedure. This third experiment aimed to strengthen previous results and compare the inversion effect for faces to the effect for a non-face highly familiar category, namely pictures of cars (Busigny & Rossion, 2010). It is known that non-face categories also elicit inversion costs in matching or recognition tasks, albeit of smaller magnitude than faces (e.g., Leder & Carbon, 2006; Robbins & McKone, 2007; Rossion & Curran, 2010; Scapinello & Yarmey, 1970; Valentine & Bruce, 1986; Yin, 1969). The question here was to test whether the patient presented any inversion effect at all, or if this peculiar effect was specific to the category of faces. In this third experiment, we used a simultaneous two-alternative force choice matching task. One full front and one 3/4 profile gray scaled photographs of 36 faces (18 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 the upright and inverted orientation. Participants had to choose between two 3/4 profile probes located at the bottom of the screen which one was the same as the full front target presented at the top of the screen. Each trial ended by the response of the participant and was followed by a 1000 ms ISI. Participants were instructed to select one of the two faces or cars that was the same as the previously shown target, by pressing a keyboard key (left or right) corresponding to the location of the target face. 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 stimuli subtended approximately $7.1^\circ \times 5.7^\circ$ for the faces and $5^\circ \times 7.8^\circ$ for the cars, on a white background.

Control participants. Nine healthy controls were tested (6 males; mean age: 61.89; SD: 7.2).

Results and discussion. Regarding faces, the control participants presented a strong face inversion effect on accuracy [upright faces: 93.2% (SD: 5.03), inverted faces: 67.9% (SD: 9.22); t_8 = 8.29, p < 0.001] and on correct response times [upright faces: 3112 ms (SD: 1325), inverted faces: 4986 ms (SD: 2858); t_8 = 3.24, p < 0.01]. Compared to normal controls, GG was impaired for accuracy at the upright orientation (63.9%; t = 5.53, p < 0.001) but he was as fast as controls (3271 ms; t = 0.114, p = 0.46). With inverted faces, his performance was within the normal range for both accuracy (63.9%; t = 0.413, p = 0.35) and correct response times (3591 ms; t = 0.463, p = 0.33) (Fig. 19A and B). In total, he did not present any face inversion effect, nor in accuracy (t_{70} = 0, p = 0.5), neither in correct RTs (t_{42} = 0.949, p = 0.17).

For pictures of cars, control participants did not show a significant inversion effect in terms of accuracy [upright cars: 95.1% (SD: 3.87), inverted cars: 94.1% (SD: 2.93); t_8 = 1.00, p = 0.174] but they did so in terms of correct RTs [upright cars: 2299 ms (SD: 1173), inverted cars: 2633 ms (SD: 1092); t_8 = 3.08, p < 0.01]. GG performed extremely well in the upright cars condition, but not significantly better than controls (97.2%; t = 0.529, p = 0.310). He also obtained a good score on accuracy in the inverted cars condition (91.7%; t = 0.800, p = 0.065), and like the controls, he did not show a significant car inversion effect in accuracy (t_{70} = 1.022, p = 0.16). Regarding RTs for cars, GG did not differ from controls at any orientation (upright cars: 2080 ms, t = 0.177, p = 0.43; inverted cars: 2755 ms, t = 0.106, p = 0.46). Hence, like controls he presented a significant inversion effect in correct RTs for cars (t_{62} = 4.141, p < 0.001).

The indexes of inversion effects for faces and cars based on the inverse efficiency (cfr supra) indicate that GG was the only participant who showed a tendency for a larger inversion index for cars than faces (Fig. 19C). In contrast, all normal participants presented a stronger inversion effect for faces than for cars. Notably, GG's car inversion index (16.83%) was in the normal (upper) range (mean: 8.09, SD: 6.17; t = 1.344, p = 0.11), while his face inversion index (4.65%) was significantly below normal controls (mean: 34.8, SD: 11.11; t = 2.575, p < 0.05).

In conclusion, GG's profile of performance was comparable to the one in normal observers when matching pictures of upright cars across viewpoint changes. In contrast, GG behaved completely differently from controls when he processed faces. This demonstrates once again the high selectivity of his impairment for faces, even when having to recognize exemplars of a visually homogenous category across viewpoint changes, he performed in the normal range. Regarding inversion, GG does not present an effect of inversion for faces, in line with the two previous experiments reported. This is also in line with the absence of inversion effect for the prosopagnosic patient PS tested extensively with upright and inverted faces (Busigny & Rossion, 2010), as well as for other such patients (e.g., Boutsen & Humphreys, 2002; Delvenne et al., 2004; McNeil & Warrington, 1991; see Busigny & Rossion, 2010). Hence, acquired prosopagnosia seems to affect primarily a process that is specific to the upright face orientation.

The absence of inversion effect cannot be explained by a general factor either since GG presented a normal inversion effect for photographs of cars. Thus, these data indicate that the inversion effect observed for faces and to (a lesser extent) to nonface objects in normal viewers (Yin, 1969) truly reflect qualitatively different functional processes rather than just quantitative differences: the effect for faces can be selectively abolished following acquired prosopagnosia.

3.5.2.5. Experiment 23. Whole-to-part effect. Rationale. Here we aimed to provide further evidence for the patient GG's deficient holistic processing mode of individual faces. A paradigm that is classically used is referred to as the whole/part advantage (Tanaka & Farah, 1993). It refers to the finding of superior discrimination of two whole faces differing by one feature (e.g., the eyes) than when two features are presented in isolation. In other words, the discrimination of the diagnostic feature is facilitated by the presence (and correct organization) of the remaining facial features. This effect is thought to reflect the fact that a change of one diagnostic feature affects the whole face, thus making the discrimination easier (Tanaka & Farah, 1993).

Various tasks of whole/part advantage were used with prosopagnosic patients: classical task of whole/part advantage in two-alternative forced choice matching tasks (Davidoff & Landis, 1990; Delvenne et al., 2004; Wilkinson et al., 2009) or in same/different decision task (De Gelder & Rouw, 2000b), variant with thatcherized faces (Boutsen & Humphreys, 2002; Riddoch et al., 2008), or identification of faces as wholes or as parts (De Gelder, Frissen, Barton, & Hadjikhani, 2003). All these studies

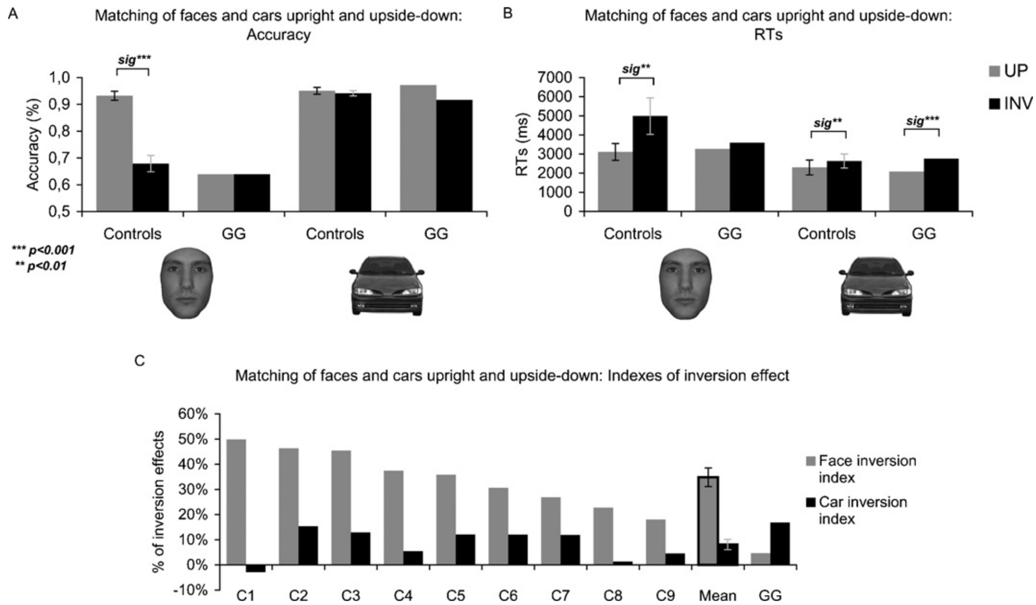

Fig. 19. Results of GG and age-matched controls in experiment 22: simultaneous matching of faces and cars upright and upside-down. (A) Accuracy rates. (B) Correct response times. (C) Indexes of inversion effect calculated on inverse efficiency (RTs/accuracy) for each single participant for both face and car condition. Bars represent standard errors.

showed that the prosopagnosic patients were impaired in showing an advantage to process whole faces in comparison with single parts.

Here, we assessed this effect in delayed face matching task, as in most studies with normal observers (e.g., Goffaux & Rossion, 2006; Michel, Caldara, & Rossion, 2006). We presented whole and parts of faces preceded by whole faces, and we completed the paradigm by also presenting trials in which the first stimulus could be a part of a face followed by whole or parts of faces (Fig. 20). The diagnostic cue for analysis was the eyes, but there were foil trials for mouth and nose (see Michel, Caldara, et al., 2006). The prediction was that, for normal observers, the performance would be better (higher accuracy, slower RTs) when encoding format (i.e. that of the target) and probe format (i.e. subsequently presented test stimuli) were identical. That is, the conditions "part-to-part" and "whole-to-whole" should have been associated with superior performance as compared to "part-to-whole" and "whole-to-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, would be influenced by the presence of the other features (see Leder & Carbon, 2005). The task used here was used and described previously in Ramon et al. (2010).

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 among 20 of the original faces. The remaining 10 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, but (as in our previous studies with this paradigm; e.g., Goffaux & Rossion, 2006; Michel, Caldara, et al., 2006; Ramon et al., 2010) were not analyzed. The task was a delayed two-alternative forced choice identity matching. Trials began with a target face 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-to-Wholes and Whole-to-Parts conditions) or a single feature (Part-to-Parts and Part-to-Wholes 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, with the remaining one (i.e., foil) differing from the target by a single feature only (eyes in experimental trials, nose or mouth in catch trials). In the *part display* condition, the probes depicted isolated face features (eyes in experimental trials, nose or mouth in catch trials). For whole faces, one probe was identical to the target and the other (i.e., foil) differed by one feature only (eyes in experimental trials, nose or mouth in catch trials). For isolated parts, the probes depicted isolated facial features (eyes in experimental trials, nose or mouth in catch trials); one of the probes was identical to the target feature (as presented in the target face), the other representing a foil. The experiment was a 2×2 within-subject design with encoding condition (Whole *vs.* Part) and retrieval (Wholes *vs.* Parts) as factors. 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 trials (four blocks of sixty trials). Trial order was at random and varied for each participant. Six practice trials were completed before the experiment commenced. The target stimulus subtended $5^\circ \times 6^\circ$ of visual angle while for the subsequently presented probes differed depending on probe type (whole faces: $4.1^\circ \times 4.1^\circ$; eye feature stimuli: $0.7^\circ \times 4^\circ$; nose features: $1.4^\circ \times 1.4^\circ$; mouth features: $1^\circ \times 2^\circ$). All stimuli were presented on a gray background.

Control participants. Nine healthy males were tested (mean age: 61.9; SD: 5.1).

Results and discussion. The data of age-matched controls are illustrated in Fig. 21A and B. The age-matched controls showed a significant advantage in the *Whole-to-whole* as compared to the *Whole-to-part* condition ("Whole-part advantage") with respect to accuracy (Whole-to-whole: 83.5%, SD: 10.14; Whole-to-part:

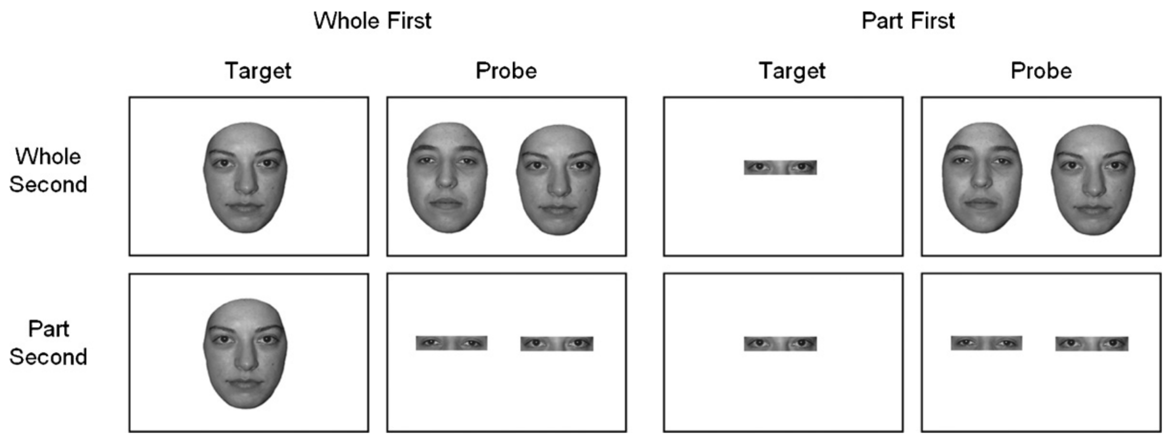

Fig. 20. Example of stimuli used in experiment 23: whole-to-part effect.

78.6%, SD: 11.19; $t_8 = 2.257$, $p < 0.05$) and correct RTs (Whole-to-whole: 1352 ms, SD: 283; Whole-to-part: 1763 ms, SD: 260; $t_8 = 11.698$, $p < 0.001$). They also showed a significant "Whole-part disadvantage" when comparing the *Part-to-part* and the *Part-to-whole* conditions, both in terms of accuracy (Part-to-part: 93.9%, SD: 5.76; Part-to-whole: 86.4%, SD: 9.27; $t_8 = 2.917$, $p < 0.01$), and correct RTs (Part-to-part: 1258 ms, SD: 208; Part-to-whole: 1564 ms, SD: 292; $t_8 = 5.48$, $p < 0.001$). These results show that the control participants are better and faster when the encoding and retrieval face context is the same.

GG showed no difference between the *Whole-to-part* and the *Whole-to-whole* conditions, neither in accuracy (Whole-to-whole: 63.8%; Whole-to-part: 68.8%; $t_{158} = 0.665$, $p = 0.25$) nor in correct RTs (Whole-to-whole: 1336 ms; Whole-to-part: 1341ms; $t_{99} = 0.076$, $p = 0.47$). He even showed a reverse trend of effect in accuracy: he was less efficient for the *Whole-to-whole* condition as compared to the *Whole-to-part* (Fig. 21A). Considering the *Part-to-part* and the *Part-to-whole* conditions, GG showed no effect in accuracy (Part-to-part: 95%; Part-to-whole: 92.5%; $t_{158} = 0.650$, $p = 0.26$), but he obtained a significant difference in the right direction in RTs (Part-to-part: 1232 ms; Part-to-whole: 1398ms; $t_{141} = 3.791$, $p < 0.001$) (Fig. 21B).

Indexes were computed using the same formula that was used for the inversion effect (cfr supra). Thus we calculated an index for the condition in which the whole face is firstly presented (inverse efficiency Whole-to-part–Inverse efficiency Whole-to-whole)/(inverse efficiency Whole-to-part + inverse efficiency Whole-to-whole) and for the condition in which the part is firstly presented (inverse efficiency Part-to-whole − inverse efficiency Part-to-part)/(inverse efficiency Part-to-whole + inverse efficiency Part-to-part). In the *whole display* condition, each single control participant obtained a high index of whole-part advantage (mean = 16.7%, SD: 7.28), but this was not the case for GG, who even obtained a negative index (−3.6%), significantly different from the controls ($t = 2.641$, $p < 0.05$) (Fig. 22A). Similarly, in the *part display* condition, each single participant showed a high index of part-whole disadvantage (mean = 14.9%, SD: 5.17). Even if GG did not show a significantly reduced effect in comparison to the controls, his effect was the lowest of them all (GG: 7.6%, controls range: [25.4–8.6%], $t = 1.332$, $p = 0.11$) (Fig. 22B).

Finally, we computed together the results of the two display conditions (*whole first* and *part first*) to obtain a general index of context change. To obtain this, we put together the condition *part-to-part* with the condition *whole-to-whole* in a new condition called "same context", and the condition *part-to-whole* with the condition *whole-to-part* in a new condition called "different context". Then we used the following formula: (same context − different context)/(same context + different context). By doing that, we calculated the percentage loss of performance when the context changes. The indexes were calculated for inverse efficiency as previously described. The results indicate that every single control participant showed a high index of context change (mean = 15.8%, SD: 3.74), while GG showed a highly reduced effect (3%, $t = 3.244$, $p < 0.01$) (Fig. 22C).

In conclusion, the age-matched controls show better performance when encoding format and recognition format are congruent: (1) when they are presented at encoding with a whole face, they have an advantage recognizing a part embedded in a whole face in contrast to the part presented in isolation (because of a whole context advantage); (2) when they are presented at encoding with a face part, they recognize the part better when presented in isolation than when it is embedded in a whole face (because of a whole context interference). In contrast, GG does not show any of these effects: he shows no whole context advantage, even presenting a reverse trend, and he presents reduced whole context interference. Most importantly, GG does not show a general effect of context change. These results mean that GG does not present the normal effects associated with a processing of the whole face configuration. These observations provide direct evidence that GG does not show a classical whole-part effect, and that he processes faces qualitatively differently than normal observers.

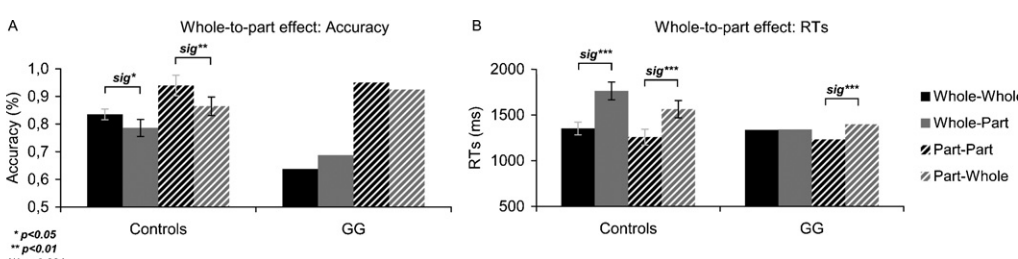

Fig. 21. Results of GG and age-matched controls in experiment 23: whole-to-part effect. (A) Accuracy rates. (B) Correct response times. Bars represent standard errors.

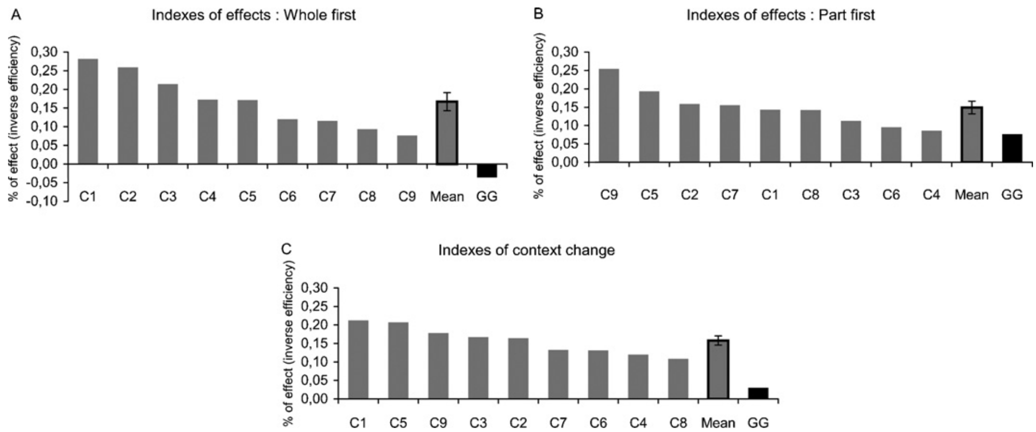

Fig. 22. Indexes of effects calculated for each single participant in experiment 23: whole-to-part effect. (A) Indexes of effect for conditions in which a whole face was presented first. (B) Indexes of effect for conditions in which a part of a face was presented first. (C) General inference indexes calculated between conditions in which context was same and different. Indexes were calculated on inverse efficiency (RTs/accuracy). Bars represent standard errors.

3.5.2.6. Experiment 24. Composite face effect: top composite (alignment × identity). *Rationale.* The composite face effect was originally described by Young et al. (1987) as the difficulty to identify either the top half (above the nose) of bottom half of a famous face when it is aligned with the other half. 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 has been successfully applied to the processing of individual faces, in which two identical top halves of faces are perceived as being slightly different if they are aligned with distinct bottom halves (Le Grand, Mondloch, Maurer, & Brent, 2004; Michel, Rossion, Han, Chung, & Caldara, 2006; Goffaux & Rossion, 2006).

One case of prosopagnosia, PS, was recently tested with several tasks of composite face effect (Ramon et al., 2010) and the results showed that she did not present the classical interference effects. Here, we used one task described in Ramon et al. (2010, experiment 5), aimed at measuring the composite face effect for GG and control participants in a matching task. We had four "same" conditions in which the top half of the faces is the same (aligned/same bottom, aligned/different bottom, misaligned/same bottom, misaligned/different bottom) and two "different" conditions in which the top is different (aligned/different top and bottom; misaligned/different top and bottom) (Fig. 23). We expected to observe a composite effect in normal controls in the *aligned/different bottom* condition, which should be revealed in two ways: by an effect of *alignment* (when the bottom is different, the effect will appear in the aligned condition, but not in the misaligned one—i.e. the classically defined composite effect), and by an effect of *identity* (in the aligned condition, the illusion will only appear when the bottom is different). By means of this paradigm, we expected to obtain an interaction between the two factors alignment and identity for normal controls. In contrast, GG should not show any advantage irrespective of condition and further that there would be no interaction between alignment and identity.

Material and procedure. The stimuli used in this experiment were color full-front 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 (Fig. 23). 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. Each original face was transformed into two composite stimuli: the first one differed from the original merely by means of an inserted gap (same top/same bottom), the second one had the same top part combined with a different bottom part from a randomly selected other face (same top/different bottom). The resulting composite stimuli were manipulated in order to create misaligned versions 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. For the "same" condition four possible trials were

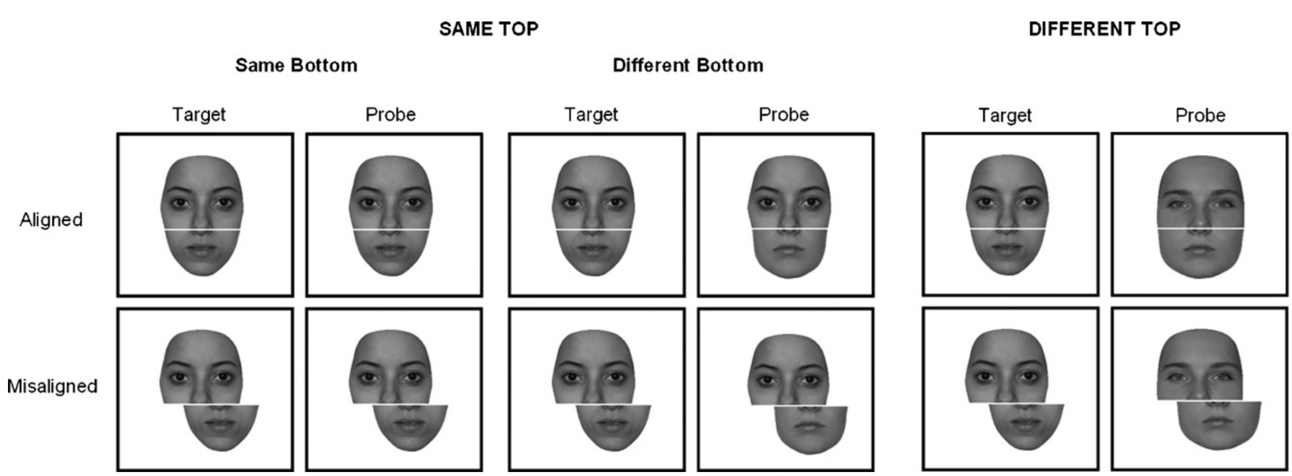

Fig. 23. Example of stimuli used in experiment 24: composite face effect.

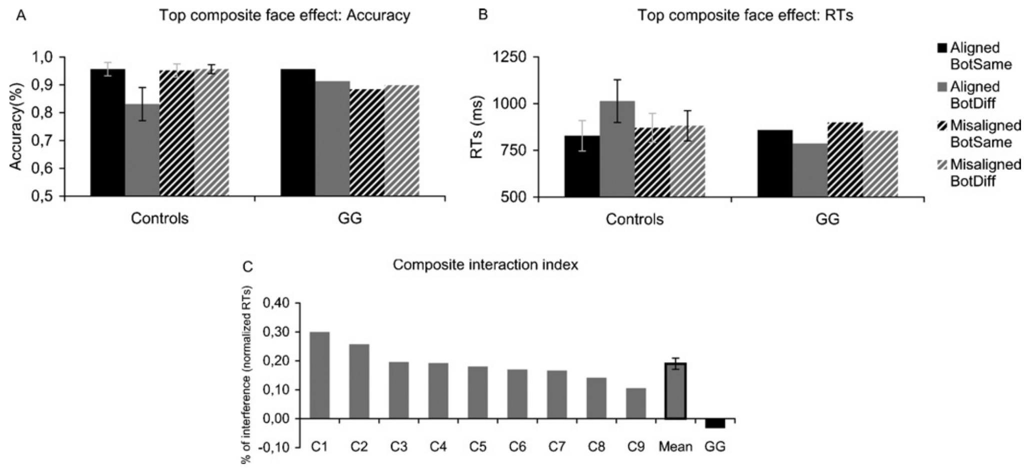

Fig. 24. Results of GG and age-matched controls in experiment 24: composite face effect. (A) Accuracy rates. (B) Correct response times. (C) Indexes of composite effect calculated on normalized RTs for each single participant. Bars represent standard errors.

created: the original face was paired with itself (*aligned/same bottom* and *misaligned/same bottom*) and its combined version with a different bottom (*aligned/different bottom* and *misaligned/different bottom*). With respect to the "different" condition, each aligned face was paired with another, randomly selected, aligned one (*aligned/different top and bottom* condition); the same was done for misaligned faces (*misaligned/different top and bottom* condition). This task was used in a previous study and was shown to be highly sensitive to disclose a composite face effect in normal participants (Ramon et al., 2010).

Participants performed a two-alternative forced choice decision task. Each trial involved the consecutive presentation of two composite 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). 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 same or different (by pressing a right or left key, respectively). The experiment consisted of a total of 138 trials, which 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 $5.7^{\circ} \times 3.8^{\circ}$ of visual angle and misaligned stimuli were $5.7^{\circ} \times 5.2^{\circ}$.

Control participants. Nine healthy males were tested (mean age: 62.44; SD: 5.12).

Results. The data of age-matched normal controls are illustrated in Fig. 24A and B. The ANOVA for accuracy rates showed a significant main effect of *alignment* ($F_{(1,8)} = 5.26$, $p < 0.05$), and a significant main effect of *identity* ($F_{(1,8)} = 5.69$, $p < 0.05$). Moreover, there was a significant interaction between the two factors ($F_{(1,8)} = 4.21$, $p < 0.05$): the performance decreased when the two parts were aligned and when the bottom was different. The ANOVA for RTs showed a marginal main effect of *alignment* ($F_{(1,8)} = 2.98$, $p = 0.061$), and a significant main effect of *identity* ($F_{(1,8)} = 7.74$, $p < 0.05$). Most importantly, in line with the results for accuracy scores, there was a highly significant interaction between the two factors ($F_{(1,8)} = 23.39$, $p < 0.001$). These findings are a hallmark of holistic face processing for control participants.

In contrast, GG obtained a profile completely different from that of the age-matched controls. Regarding accuracy, GG did not show any main effect, neither for *alignment* ($F_{(1,272)} = 1.634$, $p = 0.1$), nor for *identity* ($F_{(1,272)} = 0.182$, $p = 0.34$). Furthermore there was no interaction between the two factors ($F_{(1,272)} = 0.726$, $p = 0.20$) (Fig. 24A). With respect to correct RTs, GG showed significant effects but in the opposite direction from controls. First, he showed a main effect of *alignment* ($F_{(1,237)} = 2.807$, $p < 0.05$), but the effect was in favor of aligned stimuli (mean aligned = 822 ms < mean misaligned = 876 ms). Second, GG also obtained a main effect of *identity* ($F_{(1,237)} = 3.310$, $p < 0.05$), but again in the opposite direction from the controls (mean BotSame = 879 ms > mean BotDiff = 820 ms) (Fig. 24B). Third, and also in contrast to controls, there was no interaction between the two factors ($F_{(1,237)} = 0.178$, $p = 0.34$).

Finally, interference indexes were computed by using an interaction formula: (Aligned Botsame − Aligned Botdiff) − (Misaligned Botsame − Misaligned Botdiff). The indexes were calculated on the standardized correct response times. Each single participant obtained a high index of interference (mean = 19%, SD: 5.82), except GG than even obtained a negative index (−3.2%), significantly different from controls ($t = 3.619$, $p < 0.01$). These results clearly indicate that, contrary to normal participants, GG does not show the normal interference index (Fig. 24C).

In conclusion, the results showed, as hypothesized, clear composite integration effects in all the control participants. In contrast, GG presented with a very different performance pattern, characterized by the complete absence of composite effects. This suggests that, for GG, there is no integration between the top part and the bottom part of an individual face.

Altogether, the results collected in the face inversion, whole-part and composite face experiments show that GG has lost the ability to process holistically the individual face. He does not benefit from processing faces in the upright orientation, and his processing of a facial part is not influenced (positively or negatively) by the position and presence of the other face parts.

4. General discussion

In the present paper, we aimed at addressing the following issue: can the visual recognition impairment in prosopagnosia be truly restricted to faces, and at the same time affect the ability to process holistically? This issue is particularly important, since previous accounts that have documented prosopagnosia in terms of a holistic/configural processing deficit usually defined the disorder as a general visual recognition impairment and were based on case reports of patients who presented with a general visual agnosia (e.g., Behrmann & Kimchi, 2003; Boutsen & Humphreys, 2002; Delvenne et al., 2004; Gauthier et al., 1999; Levine & Calvanio, 1989; Saumier et al., 2001; Spillmann et al., 2000).

To address this issue, we reported an extensive neuropsychological and psychophysical investigation of GG, a new case of prosopagnosia following right hemisphere damage. To summarize, the present paper demonstrates that this prosopagnosic patient has preserved (1) recognition of nonface objects, (2) holistic processing of nonface items (Navon effect, 3D impossible figures; dot configurations), (3) fine-grained discrimination/recognition of individual exemplars of nonface objects (morphed cars, individual exemplars of birds, chairs, houses, and butterflies differing by relative distances between features), and (4) detection of faces even when holistic processing is required (visual scenes, Mooney and Arcimboldo stimuli). The patient showed normal performance and speed at all the tasks measuring these abilities. However, he is profoundly impaired in recognition/discrimination of individual faces, and this impairment is associated with a disruption of holistic processing for individual faces (inversion, whole-part and composite effects, perception of relative distances between face features defining identity, and processing of diagnostic information located on the eyes region). We discuss the theoretical implications of these findings below.

4.1. Brain damage can selectively impair face recognition

We showed that GG's visual recognition impairment is truly restricted to the category of faces. That is, object recognition is performed in the normal range, even when recognition of individual exemplars is required. GG was not only as accurate as normal controls at performing these tasks, but he performed as fast as controls, which is quite impressive considering that brain damage patients may be generally slowed down (Benton, 1986), and that GG has a complete left hemianopsia. More specifically, together with our recent studies carried out with the patient PS (Busigny et al., 2010), these data provide further evidence against the view that acquired prosopagnosia can be accounted for in terms of a general impairment in discriminating/recognizing items belonging to a visually homogeneous category (Damasio et al., 1982; Faust, 1955; Gauthier et al., 1999).

As mentioned in the introduction, GG is certainly not the first and only case of acquired prosopagnosia whose impairment is restricted to the category of faces (see Table 1 and Section 1 for references of previous studies). However, such case studies remain rare, and the specificity of the visual recognition impairment of most previous published cases remains debatable. Indeed, object recognition abilities of such patients are usually not tested extensively and/or compared to appropriate samples of normal observers, and the patient's speed is usually not measured. For instance, among the set of prosopagnosic patients reported during the past 30 years (more than a hundred), a number of those who were described as presenting with a face-specific recognition impairment also had, in fact, difficulties at object recognition (e.g., Bruyer et al., 1983; Eimer & McCarthy, 1999; McNeil & Warrington, 1991; McNeil & Warrington, 1993; Sergent & Signoret, 1992a; Whiteley & Warrington, 1977). Moreover, none of the studies reporting supposedly pure cases of prosopagnosia (see Table 1) took into account the recording of response times in their assessment of the patient's object recognition abilities (except Schiltz et al., 2006 for the patient PS). In addition, many of these latter studies did not test subordinate-level recognition of object categories (Bukach et al., 2006; Buxbaum et al., 1996; De Renzi, 1986a; De Renzi & di Pellegrino, 1998; Takahashi et al., 1995). Finally, previous studies did not address in a systematic and parametric way the issue of whether prosopagnosia reflects a general difficulty in processing visually similar items, unlike what was performed here with the patient GG.

The present case study thus provides perhaps the most convincing and unambiguous answer to the long-standing question of the specificity of prosopagnosia postulated initially by Bodamer (1947) and heavily debated for decades: *following brain damage, visual recognition impairment can truly be restricted to the category of faces*.

The implication for the understanding of normal visual face recognition is straightforward: there are processes in the human brain that are *necessary* to recognize individual faces efficiently, while these processes are not strictly necessary for visual recognition of nonface objects.

4.2. The nature of acquired prosopagnosia

The results of the present study show that GG's impairment is perceptual and not only mnesic: besides the inability to identify famous and familiar faces, he was impaired at discriminating/matching pictures of individual unfamiliar faces in many experiments. Admittedly, in most of these experiments, there was a brief delay between the first presentation of a target item, and then the target and its distractor (delayed matching, or recognition tasks). However, in some experiments, all individual faces were presented simultaneously (Benton Facial Recognition Test; experiment 4 with faces under different viewpoints; experiment 22 with inverted faces).

Following the initial concern about the specificity of the disorder and the locus of brain lesions causing prosopagnosia, this issue of the perceptual as opposed to mnesic nature of the face recognition impairment has also been debated for long. While some authors argued that prosopagnosia is primarily a memory defect (Benton, 1980; Damasio et al., 1982; Warrington & James, 1967; see also Milner, 1968), others have rather emphasized the perceptual nature of the disorder (e.g., Davidoff & Landis, 1990; De Renzi, Faglioni, & Spinnler, 1968; Delvenne et al., 2004; Farah, 1990, 2004; Hécaen, 1981). Yet, others have proposed that they are different kinds of prosopagnosia, depending on the lesion site and the functional level at which face recognition breaks down (e.g., De Renzi, 1986a; De Renzi et al., 1991; Gross & Sergent, 1992; Schweich & Bruyer, 1993; Sergent & Signoret, 1992a). However, the case of GG and of other prosopagnosic patients studied in depth in the neuropsychological literature suggests that clear-cut functional distinctions, such as the one between an apperceptive and an associative kind of prosopagnosia, appear to be elusive (Farah, 1990, 2004). Rather, the variety of functional deficits documented in prosopagnosia is likely to reflect various degrees of impairment rather than functionally dissociable types of impairment. This view is supported by the observation that most if not all prosopagnosic patients, even when different sites of lesion, extents of lesion and aetiologies of brain damage are considered, appear to be impaired to different extents on the same high-level perceptual process: holistic/configural perception of individual faces.

Prosopagnosic patients suffer from a holistic/configural impairment, in the sense that they are unable to integrate individual components into coherent global representations (Boutsen & Humphreys, 2002; Davidoff & Landis, 1990; Delvenne et al., 2004; Farah, Levinson, et al., 1995; Farah, Wilson, et al., 1995; Levine & Calvanio, 1989; Riddoch & Humphreys, 1987; Saumier et al., 2001; Sergent & Villemure, 1989; Spillmann et al., 2000). Most of the time, these patients fail at tasks measuring holistic/configural processing of both nonface items (visual closure, Navon effect, perception of 3D figures, . . .) and faces (face inversion effect, whole-part face advantage, . . .). Notorious cases are the patients LH and HJA, who were presented as visual agnosics and prosopagnosics in different reports (LH: Farah, Wilson, et al., 1995; Levine et al., 1980; HJA: Boutsen & Humphreys, 2002; Riddoch & Humphreys, 1987).

In contrast, here we report an extensive case study of a patient who presents with a normal profile of performance in holistic/configural processing of nonface items, yet who does not present with holistic/configural processing of individual faces. Therefore, should we consider that GG has a disorder that is different from what has been previously reported in other prosopagnosic patients? Or is there a common underlying explanation for their deficits?

With respect to individual faces, there appears to be common underlying difficulties between patient GG and the other cases of (prosop)agnosia mentioned above. That is, when they have to recognize an individual face, the patients focus on one part of the face at a time (e.g., the mouth) and analyze its diagnosticity, without being influenced by the other parts of the face. Hence, contrary to normal observers, face recognition in these patients is based on an independent analysis of face parts (Saumier et al., 2001; Sergent & Signoret, 1992a; Sergent & Villemure, 1989). It follows that they cannot benefit from, or be disadvantaged by, the presence of the other facial parts (Boutsen & Humphreys, 2002; De Gelder & Rouw, 2000a; Delvenne et al., 2004; Joubert et al., 2003). When the "part" is made of half a face, as in the composite face paradigm, the other half has no – or little – influence on the patient's performance (Ramon et al., 2010; the present study, experiment 24). Moreover, since inversion disrupts a holistic process (Farah, Wilson, et al., 1995; Rossion, 2009; Van Belle, de Graef, Verfaillie, Rossion, & Lefèvre, 2010) that is already absent for such patients, their individual face recognition abilities do not suffer much from inversion (e.g., Busigny & Rossion, 2010; Farah, Wilson, et al., 1995; Marotta et al., 2002).

However, despite this common underlying difficulty, the performance of such patients in face recognition tasks may be contaminated by more general visual recognition impairments and thus should be interpreted with great care. In contrast, when the face recognition impairment can be isolated, which is the case for patient GG, we believe that the nature of prosopagnosia can be circumscribed and understood more directly.

The best support for the isolated nature of GG's deficit comes from the fact that he was able to perceive a face as a face, even when it required holistic processing. Such intact performance at categorizing Mooney and Arcimboldo facelike stimuli is unlikely to occur in general visual integrative agnosia. The results of these experiments thus indicate that what truly differs between the preserved and impaired face processing functions in GG is the *level* at which processing occurs: the patient is impaired at individual face recognition, but not at face detection. Why is he not impaired at individual recognition of nonface objects then? The answer seems quite simple: recognition of individual exemplars of nonface objects does not *require* holistic processing, even in normal observers. In fact, recognition of individual exemplars of nonface objects is quite rare in real life circumstances for most observers, and may be largely based on identifying fine-grained details and local diagnostic parts rather than using the whole of the object (Biederman & Kalocsai, 1997).

Given these considerations, and although it seems to be a strong claim, we would like to argue that all acquired prosopagnosic patients present with at least some impairment of holistic/configural processing of individual faces. Almost all patients who were tested in the literature with paradigms evaluating holistic/configural face processing showed deficits at this level. In fact, we know of only a few cases of prosopagnosia who were reported to have at least partial preservation of holistic/configural processing of individual faces and we believe that the evidence of entirely normal holistic processing was not demonstrated in these cases (see Ramon et al., 2010). Two cases reported by Sergent and colleagues (PV, Sergent & Poncet, 1990; PC, Sergent & Signoret, 1992a) showed evidence for holistic processing in a matching task of faces differing by one or several features: their performance indicated that the processing of one feature was influenced by the presence of the other features. However, in light of recent advances in the field of memory-related person recognition disturbances (e.g., Gainotti, 2007), the first patient appears to present with a general semantic disorder rather than prosopagnosia. Such cases of semantic memory impairment related to person knowledge may indeed present with largely preserved holistic face processing (Busigny, Robaye, Dricot, & Rossion, 2009). The second patient was largely impaired at perceiving faces but, according to the authors he had "*not completely lost the basic mechanisms that underlie the normal perceptual operations on facial representations*" (Sergent & Signoret, 1992a, p. 385). However, it remains unclear based on a single experiment whether this patient's holistic face processing was entirely intact when compared to normal observers. A recently described case of prosopagnosia (LR) is particularly interesting for this issue (Bukach et al., 2006). The authors argued that LR had preserved holistic face processing because he showed interference in a variant of the composite face task. However, there is evidence that LR's ability to process individual faces holistically is not fully preserved. For instance, he has an abnormal inversion effect for changes at the level of the eyes, and he has been described as unable to consider multiple features of a face altogether, focusing on the mouth at the expense of the eyes, or vice-versa (Bukach et al., 2006). He can also show slow processing of inter-feature distances as compared to local feature changes – a pattern which can be interpreted as a malfunctioning holistic face processor (Rossion et al., 2009). Finally, even though his impairment in individual face matching tasks appears to be less severe than PS, or than the patient GG reported in the present paper, we have been collecting data recently showing that the same patient LR clearly presents with impairment in holistic perception of the individual face. This claim is supported by a reduced face inversion effect, whole-part advantage, and composite face effect with the same paradigms as used here (Busigny et al., in preparation). Moreover, eye-gaze contingency experiments (see Van Belle, de Graef, Verfaillie, Busigny, et al., 2010) performed with this patient indicates a reduced perceptual field in individual face matching, suggesting that he has to focus on one feature at a time when individualizing faces.

Therefore, in our view there is no clear evidence in the literature of prosopagnosic patients who show complete preservation of holistic face processing. Rather than suggesting that holistic processing of individual faces is *completely* abolished in all cases of prosopagnosia, we propose that holistic processing of individual faces may be disrupted to variable extents in these patients, preventing them from perceptually encoding individual faces accurately and rapidly.

In summary, GG is a pure case of prosopagnosia following brain damage who is impaired at perceiving an individual face holistically. The nature of his prosopagnosia is characterized by his inability to perceive an individual face as a global and integrated pattern: he has to analyze each facial feature separately, as if all features were isolated. While such a process seems to be necessary for face recognition, it does not appear to be necessary for object categorization, either at basic and more fine-grained levels.

4.3. "Specific" does not necessarily mean "modular" in holistic face processing

Based on the present case study, we conclude that holistic processing of the individual face is impaired in prosopagnosia, and thus that this ability is necessary for normal face recognition. Importantly, this observation does not necessarily imply that the impaired processes were *selectively* engaged for faces before brain damage occurred. One cannot exclude that, before brain damage, these processes may have been involved also in the recognition of certain classes of nonface objects to some extent. In other words, the observation of pure cases of prosopagnosia such as GG, as well as the documentation of the reverse dissociation (e.g., Moscovitch et al., 1997), must not be misinterpreted as evidence of module for processing faces (e.g., Kanwisher, 2000). Nonetheless, case studies such as the one of GG indicate, at the very least, that such processes are not strictly necessary for object recognition. Moreover, one cannot exclude that brain processes which are necessary for face recognition but not for object recognition in normal observers, may be critical for processing nonface objects in exceptional cases of visual expertise. Indeed, recognition of items belonging to domains of visual expertise can sometimes be impaired concomitantly with faces (e.g., birds in a birdwatcher, Bornstein, 1963; calves and cows in two farmers, Assal, Favre, & Anderes, 1984; Bornstein, Sroka, & Munitz, 1969; fish in a fisherman and a fish salesman, Clarke, Lindemann, Maeder, Borruat, & Assal, 1997; Takahashi et al., 1995; plants in a florist, Clarke et al., 1997; mountains in an alpinist, Clarke et al., 1997). The literature on normal observers also support the view that visual expertise may increase holistic processing for nonface objects (e.g., dogs, Diamond & Carey, 1986; birds, Rhodes & McLean, 1990; Greebles, Gauthier & Tarr, 1997; cars, Rossion & Curran, 2010; although see Gauthier & Bukach, 2007; McKone, Kanwisher, & Duchaine, 2007; Robbins & McKone, 2007).

In order to address this issue in prosopagnosia, one would have to attempt training patients such as GG at becoming experts in visual recognition of individual items from nonface categories. If such an attempt fails, this may provide indirect evidence that the development of an unusual visual expertise with a category of nonface objects requires the same (holistic) processes that are necessary for expertise in individual face recognition. Evidently, this question is quite difficult to answer at this point in time and remains largely open.

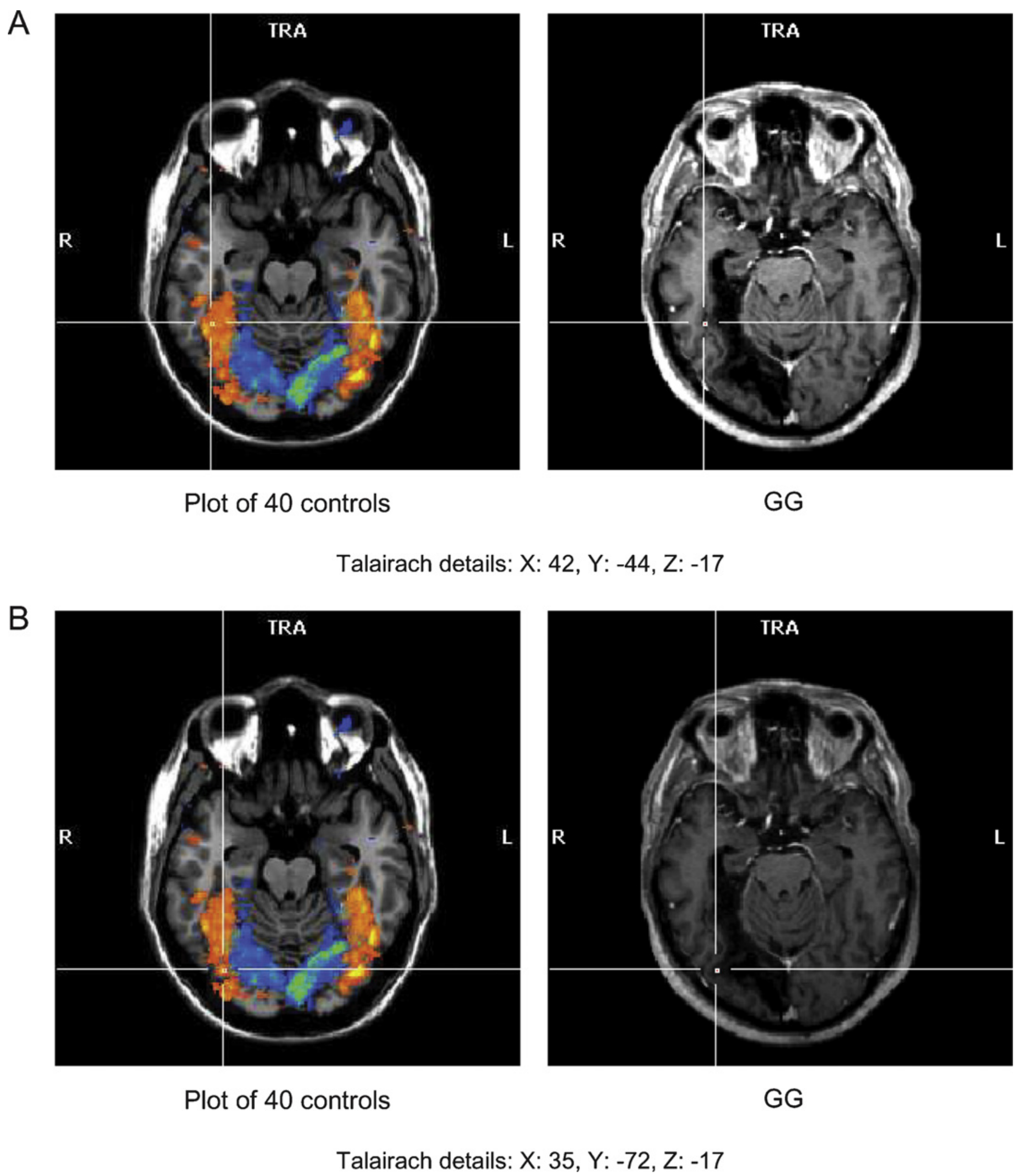

Fig. 25. Overlap of face activations in 40 normal participants as compared to GG's lesion localization. (A) Average position of the fusiform face ares ('FFA') in the 40 normal participants (Talairach details: *X*: 42, *Y*: −44, *Z*: −17). (B) Average position of the occipital face ares ('OFA') in the 40 normal participants (Talairach details: *X*: 35, *Y*: −72, *Z*: −17). The contrasts were obtained by the conjunction between faces minus objects and faces minus scrambled faces (see Dricot, Sorger, Schiltz, Goebel, & Rossion, 2008). Orange color means positive activations; blue color means negative activations. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

4.4. The neural substrates of prosopagnosia and face recognition in the human brain

The last theoretical issue for which the present case study is relevant concerns the neural substrates of prosopagnosia. Originally, and for quite a long time, the debate has been centered on the respective roles of the right and left hemispheres. Following a survey of twenty-two cases, Hécaen and Angelergues (1962) were the first to argue that the right hemisphere lesion was dominant in causing prosopagnosia. Contrary to later claims by Damasio et al. (1982), it was later clearly established that a right hemisphere lesion is sufficient in causing prosopagnosia (e.g., Barton et al., 2002; Bouvier & Engel, 2006; De Renzi, 1986b; Landis, Cummings, Christen, Bogen, & Imhof, 1986; Riddoch et al., 2008; Sergent & Signoret, 1992b; Wada & Yamamoto, 2001; Wilkinson et al., 2009). The case report of the patient GG adds up to this evidence, which does not mean however that the right hemisphere is sufficient for face recognition. Indeed, one cannot exclude that left hemispheric processes potentially important for faces are deprived of inputs from damaged right hemisphere areas in such patients, thereby contributing to increase their face recognition impairment. Yet, the right hemispheric dominance in face recognition is an established fact, supported by multiple evidence in cognitive neuroscience: faster and better performance for faces presented in the left than the right visual field (e.g., Hillger & Koenig, 1991), enhanced face-sensitivity in areas of the right compared to the left hemisphere as found in neuroimaging (e.g., Kanwisher, McDermott, & Chun, 1997; Sergent, Otha, & MacDonald, 1992), as well as in electrophysiological components recorded from the human scalp (e.g., Bentin, Allison, Puce, Perez, & Mccarthy, 1996). Behavioural and neural studies performed in non-human primates and other mammals also support this right hemispheric dominance (Peirce & Kendrick, 2002; Perrett et al., 1988; Zangenehpour & Chaudhuri, 2005). In humans, it has been related to configural/holistic perception, not only at the basic-level (Parkin & Williamson, 1987), but also and mainly at the individual level (Jacques & Rossion, 2009; Schiltz & Rossion, 2006). The present study suggests that holistic perception of the individual face depends critically on the right occipito-temporal cortex. Regarding GG, in the absence of functional neuroimaging data, it is unclear whether his ventral occipito-temporal lesions, which are quite medial, encompass two well-defined ventral areas showing face preferential response in the human brain (e.g., Fusiform face area, FFA, and Occipital Face Area, OFA; Fig. 25) or their putative direct or indirect anatomical connections. Interestingly, GG's lesions show almost no overlap with PS' lesions in the right hemisphere, which concern the territory of the right OFA in the lateral occipital cortex (see Sorger, Goebel, Schiltz, & Rossion, 2007). Moreover, the pure cases of prosopagnosia referred to above (Table 1) presents with different localization of brain damage: some patients present with quite posterior right hemispheric lesions in the occipital lobe (WB, Buxbaum et al., 1996; Anna, De Renzi & di Pellegrino, 1998; PS, Rossion et al., 2003), some have right lesions in the temporal lobe only (VA, De Renzi et al., 1991; OR, De Renzi et al., 1994) or in both the occipital and the temporal lobes (Patient 4, De Renzi, 1986a; case 3, Takahashi et al., 1995; MT, Schweinberger et al., 1995; Wada & Yamamoto, 2001; 009, Barton et al., 2004; FB, Riddoch et al., 2008; DC, Rivest et al., 2009), and one of them also has a very anterior lesion, in the right temporal pole (LR, Bukach et al., 2006). These observations are in agreement with the fact that in the normal human brain there is a whole set of areas distributed all along the ventral occipital and temporal cortex that respond preferentially or even exclusively to faces (Fox, Iaria, & Barton, 2009; Haxby, Hoffman, & Gobbini, 2000; Ishai, 2008; Pinsk et al., 2009; Rajimehr, Young, & Tootell, 2009; Sergent et al., 1992; Tsao, Moeller, & Freiwald, 2008; see also Allison, Puce, Spencer, & McCarthy, 1999). They suggest that all these areas play an important role in face recognition, and/or that they form a tightly connected functional network whose full integrity is necessary to carry out face recognition efficiently (Rossion et al., 2003; Fox, Iaria, & Barton, 2008). In this context, one may wonder how patients with different lesion localization might show a common functional impairment – perhaps to a different extent – at holistic individual face perception. One reason may be that damage to any node of the underlying distributed cortical face processing network impinges on the functional integrity of other areas of this network (Fox et al., 2008; Rossion, 2008b; Sergent & Signoret, 1992b). In this way, a critical aspect of the face processing function would always be altered, at least to a certain extent, in all prosopagnosic patients. Supporting this view, we have previously found that the right middle fusiform gyrus of the patient PS is structurally preserved and shows sensitivity to faces over other object categories ('FFA'; Rossion et al., 2003). However, this area – which is the most sensitive to holistic face perception in the normal brain (Schiltz & Rossion, 2006) – does not even present release from adaptation to identity in PS' brain (Schiltz et al., 2006), presumably lacking critical inputs from the posteriorly damaged right inferior occipital cortex. This example shows that brain regions which may appear structurally intact and thus not considered to be critically associated with the impaired function(s) in a prosopagnosic patient may in fact be functionally depressed because they do not receive normal inputs from lesioned regions ('diaschisis'; see Price, Warburton, Moore, Frackowiak, & Friston, 2001). Therefore, if face recognition is subtended by a highly distributed network of interdependent areas, predominantly in the right hemisphere, it might not be surprising that all cases of acquired prosopagnosia, despite different localization of brain damage, present relatively similar functional impairments.

5. Conclusion

We report a detailed single-case study of a new prosopagnosic patient following right unilateral damage which offers new insights in the comprehension of this clinical syndrome as well as that of normal face recognition. First, with respect to the issue of specificity, we demonstrated that face recognition can be affected selectively in acquired prosopagnosia, without affecting other categories of objects (even when these objects are very similar). Second, the basis of GG's deficit can be interpreted in terms of a selective impairment of holistic perception of the individual face, which is distinct from holistic object and face processing at the basic level. We conclude that right unilateral brain damage may lead to a specific impairment of holistic perception of individual faces, a function that appears critical for normal face recognition but not for object recognition.

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