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Acquired prosopagnosia as a face-specific disorder: Ruling out the general visual similarity account

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ABSTRACT

Prosopagnosia is classically defined as a disorder of visual recognition specific to faces, following brain damage. However, according to a long-standing alternative view, these patients would rather be generally impaired in recognizing objects belonging to visually homogenous categories, including faces. We tested this alternative hypothesis stringently with a well-documented brain-damaged prosopagnosic patient (PS) in three delayed forced-choice recognition experiments in which visual similarity between a target and its distractor was manipulated parametrically: novel 3D geometric shapes, morphed pictures of common objects, and morphed photographs of a highly homogenous familiar category (cars). In all experiments, PS showed normal performance and speed, and there was no evidence of a steeper increase of error rates and RTs with increasing levels of visual similarity, compared to controls. These data rule out an account of acquired prosopagnosia in terms of a more general impairment in recognizing objects from visually homogenous categories. An additional experiment with morphed faces confirmed that PS was specifically impaired at individual face recognition. However, in stark contrast to the alternative view of prosopagnosia, PS was relatively more impaired at the easiest levels of discrimination, i.e. when individual faces differ clearly in global shape rather than when faces were highly similar and had to be discriminated based on fine-grained details. Overall, these observations as well as a review of previous evidence, lead us to conclude that this alternative view of prosopagnosia does not hold. Rather, it seems that brain damage in adulthood may lead to selective recognition impairment for faces, perhaps the only category of visual stimuli for which holistic/configural perception is not only potentially at play, but is strictly necessary to individualize members of the category efficiently.

1. Introduction

Can recognition of faces be selectively impaired following brain damage, leaving object recognition abilities intact? This question has been of interest to neurologists, cognitive neuropsychologists and cognitive neuroscientists in general at least ever since Bodamer (1947) coined the term "prosopagnosia" to refer to "*the selective disruption of the perception of faces, one's own face as well as those of others, which are seen but not recognized as faces belonging to a particular owner*" (Bodamer, 1947, English translation by Ellis & Florence, 1990, p. 83). Providing evidence for a face-specific disorder following brain damage is important because it would apparently support the view that faces are processed specifically, and thus that at least some aspects of face processing could be studied in relative isolation with respect to general visual object recognition.

In his definition of prosopagnosia, Bodamer (1947) further stated that "the disorder appears in varying strengths and together with the most different forms of agnosia, but can be separated from these from the outset" (Ellis & Florence, 1990, p. 83). Yet, despite the accumulation of cases of acquired prosopagnosia reported over the years, this important issue of domain-specificity remains largely unclear and debated (e.g., Barton, 2008; Blanc-Garin, 1984; Damasio, Damasio, & Van Hoesen, 1982; Farah, Levinson, & Klein, 1995; Gauthier, Behrmann, & Tarr, 1999; McNeil & Warrington, 1993; Riddoch, Johnston, Bracewell, Boutsen, & Humphreys, 2008). One major reason for this lack of clarification is that, unfortunately, most cases of prosopagnosia[1] reported in the literature have not

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[1] Here the term prosopagnosia will refer to the classical neurological syndrome of acquired prosopagnosia (AP), without any reference to cases of congenital or developmental prosopagnosia, i.e. the lifelong impairment in processing faces with-

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

Authors	Case	Lesion	Objects	Faces
De Renzi (1986)	Patient 4	Right parahippocampal gyrus, lingual gyrus, fusiform gyrus, calcarine fissure, cuneus	- Figure-ground discrimination: intact - Visual closure: intact - Overlapping figures: intact - Object naming: intact	- BFRT (short form): impaired (18/27) - Memory of new faces: impaired
De Renzi, Faglioni, Grossi, and Nichelli (1991)	VA	Right temporal lobe	- Visual closure: intact - Object naming (usual & unusual view): intact - Coin discrimination: intact - Recognition of personal belongings: intact - Makes of cars naming: intact	- BFRT (short form): intact (21/27, no RTs) - Familiarity judgment: impaired - Famous faces designation: impaired
De Renzi, Perani, Carlesimo, Silveri, and Fazio (1994)	OR	Right temporal lobe involving T3, T5 & T6; right parietal lobe involving P1 & P2	- Object naming: intact - Recognition of animals, fruits, vegetables (usual & unusual views): intact - Italian coins discrimination: intact	- Matching of unknown faces: impaired - Familiarity judgment: impaired - Famous faces designation: impaired
Takahashi et al. (1995)	Case 3	Right temporo-occipital lobe, involving fusiform & lingual gyri	- Visual segmentation: intact - Gestalt completion test: intact - Kanizsa triangles: intact - Real object naming: intact	- BFRT (Japanese version): intact (42/54, no RTs) - Same/different judgment: intact - Memory of new faces: impaired - Familiar faces recognition: impaired
Schweinberger, Klos, and Sommer (1995 and Henke, Schweinberger, Grigo, Klos, and Sommer (1998)	MT	Right temporo-parietal lobe, also extending in frontal & occipital areas	- Visual segmentation: intact - Visual closure: intact - Object naming (line drawings): intact - Animals naming: intact - Similar objects naming (fruits and vegetables; symbols of German industrial brands; cars brands): intact	- BFRT: impaired (37/54, very slow) - Memory of new faces: impaired - Famous faces recognition: impaired
Buxbaum, Glosser, and Coslett (1996)	WB	Bilateral occipital lobes	- Object naming (real objects; drawings): intact - Memory for homogeneous category of objects (glasses, different views): intact	- BFRT: impaired (20/54) - Memory of new faces (different views): impaired - Famous faces recognition: impaired
De Renzi and di Pellegrino (1998)	Anna	Bilateral posterior cingulate gyrus, infra- & supracalcarine areas, mesial part of the superior parietal lobe	- Perceptual categorization: intact - Visual segmentation: intact - Visual closure: intact - Object naming (colour photographs; drawings; Snodgrass & Vanderwart): intact - Memory for homogeneous category of objects (glasses, different views): intact	- BFRT (short): intact (21/27, no RTS) - Memory of new faces (same view): intact - Memory of new faces (different views): impaired - Famous faces designation: impaired - Familiarity judgment: impaired - Famous faces recognition: impaired
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): intact - Visual segmentation: intact - Recognition of letters and symbols: intact - Object naming (real objects; pictures; line drawings; usual/unusual views): intact - Famous places naming: intact - Animal face naming: intact	- Matching unfamiliar faces: impaired - Memory of new faces: impaired - Familiarity judgment on famous faces: impaired - Famous faces recognition: impaired - Familiarity judgment on familiar faces: impaired - Familiar faces recognition: impaired
Rossion et al. (2003), Schiltz et al. (2006), Busigny and Rossion (in press)	PS	Right infero-occipital lobe and middle temporal gyrus; left mid-ventral gyrus & posterior cerebellum	- Low-level visual processing (BORB): intact - Object decision: intact - Object naming (Colored Snodgrass & Vanderwart): intact - Between- & within category discrimination: intact - Homogeneous categories (multi-parts novel objects, cars): intact	- BFRT: impaired (27/54, very slow) - WRMT: impaired - Matching unfamiliar faces (same view; different views): impaired - Familiarity judgment: impaired - Famous faces recognition: impaired

Table 1 (*Continued*).

Barton et al. (2004), Barton (2008, 2009)	009	Right occipito-temporal lobe, involving fusiform gyrus	- Low-level visual processing (VOSPB): intact - Incomplete letters: intact - Visual segmentation: intact - Navon effect: intact - Object decision: intact - Vegetable and fruit identification: intact - Dot-displacement discrimination (2 & 4 dots): intact	- Benton: intact (43/54, no RTs) - WRMT: impaired - Familiarity judgment: impaired
Bukach, Bud, Gauthier, and Tarr (2006)	LR	Right infero-anterior temporal lobe & amygdala	- Low-level visual processing (VOSPB, Benton line): intact - Silhouettes recognition: intact - Object naming (noncanonical view; Snodgrass & Vanderwart): intact	- Benton: acc intact (49/54) but RTs very slow and feature-by-feature strategy - Benton (17sec cutoff version): impaired (12/54) - WRMT: impaired - Familiarity judgment: impaired - Famous faces recognition: impaired
Riddoch et al. (2008)	FB	Right inferior occipital lobe, inferior & middle temporal lobe, fusiform gyrus	- Low-level visual processing (BORB, VOSPB): intact - Object naming (non-living; living: birds, flowers, vegetables, fruits): intact - Learning associations name/novel multipart object: intact	- Matching faces (different views): impaired - WRMT: impaired - Familiarity judgment: impaired - Famous faces recognition: impaired
Rivest, Moscovitch, and Black (2009)	DC	Bilateral medial occipital lobe, involving lingual gyrus and cuneus; right fusiform gyrus & frontal lobe	- Low-level visual processing (VOSPB): intact - Visual segmentation: intact - Object naming (Boston naming test): intact - Recognition of famous buildings: intac t- Recognition of dog breeds: intact	- Benton: impaired (40/54, impaired in comparison of age-matched controls) - Matching front view faces: intact - Matching side view faces: intact - Matching side-front faces: impaired - Famous faces naming: impaired

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

been formally tested to assess their object recognition abilities. A second reason for which this issue of domain-specificity is still debated is that a careful look at reports of some prosopagnosic patients who apparently presented with normal object recognition reveals in fact that some of these cases of "face-specific disorders" also present with object recognition impairments (e.g., FW, QL & WA, Bruyer et al., 1983; Whiteley & Warrington, 1977; WJ, McNeil & Warrington, 1991, 1993; RM, PM & PC, Sergent & Signoret, 1992; PHD, Eimer & McCarthy, 1999). Unfortunately, most of these reports of cases of acquired prosopagnosia provide insufficient information regarding the patient's object processing abilities, and/or can be criticized for methodological limitations in testing these object recognition abilities.

Considering these limitations, a brief but extensive overview of the neuropsychological literature nevertheless points to 13 prosopagnosic patients, who could potentially be considered as presenting with a face-specific recognition impairment (see Table 1). However, in reality, demonstrating that a brain-damaged patient's impairment is truly restricted to face recognition has proved problematic, for several reasons. First, one cannot be certain that the patient reported in a given study would be able to recognize *all* visually complex objects, as only a limited amount of object categories can be tested in a given study. Second, ideally, evidence for normal face and abnormal object recognition would have to be found within the same task, of equal difficulty for faces and nonface objects. Third, in order to assess the validity of a claim for a face-specific processing impairment, some may expect that the patient always performs as well as normal observers for processing nonface objects. However, low-level vision is rarely intact in cases of prosopagnosia following brain damage (e.g., upper visual field defects, achromatopsia, ... see Hécaen & Angelergues, 1962; Meadows, 1974; Barton, Cherkasova, Press, Intriligator, & O'Connor, 2004; Bouvier & Engel, 2006). Even though such low-level defects cannot explain the face recognition impairments in prosopagnosia (De Haan, Heywood, Young, Edelstyn, & Newcombe, 1995), they may affect the patients' object recognition performance in any given task. Moreover, selective attention, memory, or response planning may also be affected by brain damage in such cases, possibly worsening any performance of the patient in a given task. Fourth, in the same vein, potential cases of selective acquired prosopagnosia may be requested to perform *as fast* as normal observers at object recognition tasks performed equally well (Gauthier et al., 1999). However, irrespective of their face recognition impairment, brain-damaged patients may be slowed down in complex perceptual, cognitive and motor tasks, or be less confident about their judgment, and their response times may increase proportionally with every operation that they have to perform (see Benton, 1986). Fifth, and perhaps less importantly, some authors have pointed out that normal object recognition performance of the prosopagnosic patient should not be accountable by alternative strategies such as matching identical images that are physically identical for instance (e.g., Riddoch et al., 2008).

out acquired brain damage (e.g., Behrmann & Avidan, 2005; Duchaine, Yovel, Butterworth, & Nakayama, 2006).

Given these requirements, it can be extremely difficult to find a case of prosopagnosia for which one can fully exclude a more general visual recognition impairment. As a matter of fact, we are not aware of any single patient in the studies reported above or in the current literature, who fulfills all these criteria. This is not to say that these five issues are not important to consider, in particular when one aims at making strong statements regarding the domain-specificity of prosopagnosia. However, given the relative rarity of brain-damaged cases of prosopagnosia and the difficulties associated with the study of these patients, taking these criteria at face value may postpone the resolution of this theoretical issue for long.

Another way to address the issue of the domain-specificity of acquired prosopagnosia is perhaps to assess the validity of the alternative views. That is, if there is no such thing as a truly pure face-specific disorder following brain damage, as suggested by some authors (see below), how could one then account for the number of patients reported with brain damage to ventral posterior regions of the brain – in particular in the right hemisphere (Bouvier & Engel, 2006; Hécaen & Angelergues, 1962) – who complain of visual recognition impairments for faces only? Furthermore, why many other prosopagnosic patients reported in the literature appear to have more severe difficulties at processing faces than objects? The main alternative hypothesis to the domain-specificity view is that acquired prosopagnosia corresponds to a defect in recognizing/discriminating between members of a visually homogeneous category (Blanc-Garin, 1984; Damasio et al., 1982; Faust, 1955; Gauthier et al., 1999; Lhermitte, Chain, Escourolle, Ducarne, & Pillon, 1972). According to this view, faces (1) form a particularly homogenous visual category compared to nonface object categories, and (2) are the only visual category for which our visual recognition system *needs* to individualize its members correctly and rapidly for adequate social interactions. That is, individualization is a processing *request* that is highly specific to faces, unlike other visually homogenous categories that we encounter in daily life and for which a basic level categorization is usually largely sufficient ("a chair", "a car", "a dog", etc.). According to this alternative view then, some acquired prosopagnosic patients do not complain of object recognition impairments because they generally do not have to categorize members of nonface object categories at a fine-grained level (i.e., chair A and not chair B). However, if they would have to discriminate objects from visually similar distractors, as when members of a visual category have to be individualized, then these patients would be in trouble. This "*general categorization within a visually homogenous category*" view is a quite old alternative hypothesis to the domain-specificity account of prosopagnosia (Faust, 1955; Lhermitte et al., 1972), which has been formulated most explicitly first by Damasio et al. (1982), and more recently by Gauthier et al. (1999).

Is there any solid empirical evidence supporting this view? Damasio et al. (1982) only reported, anecdotically, that two of their prosopagnosic patients were able to recognize visual items such as "owl", "elephant" or "horse", but that they failed at recognizing different instances of visually similar cats, with some being named "tiger" or "panther". They concluded that prosopagnosia was not specific to faces but that the deficit was due to the requirement to *"evoke the specific context of a visual stimulus belonging to a visually "ambiguous" category"* (Damasio et al., 1982, p. 338). Taking over this idea within a real experimental context, Gauthier et al. (1999) tested two cases of acquired prosopagnosia in a set of visual discrimination tasks. The two patients were described as showing steeper increases of error rates and correct RTs as the visual similarity between the distractor and the target increased. These observations were taken as evidence against the domain-specificity account of acquired prosopagnosia, and in favor of the view that the syndrome should be better characterized as an impairment in discriminating items at subordinate levels of categorization (i.e., visually similar), regardless of object category.

The "*general categorization within a visually homogenous category*" is undoubtedly an interesting and elegant alternative account of the domain-specificity of acquired prosopagnosia. However, at second glance, it is, unfortunately, not very well supported by empirical evidence. First, the prosopagnosic patients tested both by Damasio et al. (1982) and Gauthier et al. (1999) all complained and presented with severe deficits at recognizing simple nonface objects, i.e. they suffered from a general visual agnosia syndrome to start with. That is, they could not even categorize objects at the basic level accurately and rapidly ("a chair"). Because of that, the two patients of Gauthier et al. (1999) made more mistakes and were slower relative to normal controls even when discriminating pictures of highly different nonface objects (e.g., dog *vs.* chair). Thus, they were certainly not the best cases of acquired prosopagnosia to test the alternative hypothesis to the domain-specificity account. Second, because of their impaired performance even at the easiest level of discrimination (e.g., discriminating the picture of a dog *vs.* a chair in about 1000 ms for prosopagnosic patients *vs.* 500 ms for normal controls), there were large baseline differences between the patients and the controls, which were not taken into account in the analyses by Gauthier et al. (1999). These authors interpreted the interactions between the groups (patients *vs.* controls) and levels of visual similarity of the distractors, without normalizing their data according to baseline differences. This kind of analysis and its interpretation are problematic. Third, neither in Damasio et al.'s (1982) anecdotal reports, nor in Gauthier et al.'s (1999) experiments, there were objective (i.e. parametric) manipulations of visual similarity of the distractors to the target to identify or match. As a result, increases in RTs and error rates were not even always observed from one level of discrimination to the next even for normal observers (e.g., see Fig. 7 in Gauthier et al., 1999), so that these authors' hypothesis could not be tested adequately.

To summarize, on the one hand, several studies have reported cases of prosopagnosia who do not complain of object recognition difficulties and can apparently recognize nonface objects even at the individual level (Table 1). However, none of these studies tested the alternative view of prosopagnosia mentioned above, considering both accuracy rates and RTs and using objective (i.e. parametric) manipulations of visual similarity. On the other hand, the alternative view of prosopagnosia as an impairment of categorization within a visually homogenous category has not been tested with appropriate brain-damaged patients experiments and analyses, thus failing to provide robust evidence to support this latter hypothesis.

In the present study, we report the strongest test to date of the hypothesis that acquired prosopagnosia may be due, or be directly related, to a general difficulty at discriminating visually similar exemplars of a nonface category. To do so, we tested a rare brain-damaged case of prosopagnosia who does not present with any complains and difficulties at basic-level object recognition, the patient PS, previously reported in many publications (first in Rossion et al., 2003). The 3 experiments of the present paper specifically test PS' discrimination of individual exemplars of nonface objects (novel shapes, common objects from multiple categories, single highly familiar category) in which the similarity of the distractor and the target item is increased parametrically, offering a direct test of the "*general categorization within a visually homogenous category*" hypothesis of acquired prosopagnosia. In the final experiment we also manipulate levels of similarity of the distractor within the category of faces, offering new perspectives on understanding the

nature of the face processing impairment that characterizes prosopagnosia.

2. Case description of PS

PS is a case of acquired prosopagnosia who has been reported in detail in several publications focusing on her behavioral and neural processing of faces (e.g. Caldara et al., 2005; Rossion et al., 2003; Ramon, Busigny, & Rossion, 2010; Sorger, Goebel, Schiltz, & Rossion, 2007). To summarize briefly, PS was born in 1950 and sustained closed head injury in 1992 that left her with extensive lesions of right inferior occipital cortex and left mid-ventral (mainly fusiform) gyrus. Minor damage to the left posterior cerebellum and the right middle temporal gyrus were also detected (see Sorger et al., 2007 for extensive anatomical details). After medical treatment and neuropsychological rehabilitation, PS recovered extremely well from her cognitive deficits following the accident. Her only continuing complaint remains a profound difficulty in recognizing familiar faces, including her own face on photographs, and family members' faces when presented out of context. To determine a person's identity, she relies on external cues such as haircut, moustache or glasses, but also on the person's voice, posture, gait, etc. She may also use sub-optimal facial cues such as the mouth or the lower external contour to recognize faces, and is particularly impaired at extracting diagnostic information from the eyes of the face (Caldara et al., 2005; Rossion, Legrand, Kaiser, Bub, & Tanaka, 2009). For discriminating faces from other objects, PS performs as well as normal participants but is impaired and slowed down at recognizing faces at the individual level (Rossion et al., 2003; Schiltz et al., 2006). Her scores at the Benton Face Recognition Test (BFRT, Benton & Van Allen, 1968) and the Warrington Recognition Memory Test (WRMT, Warrington, 1984) for faces, rank her as highly impaired (Rossion et al., 2003; Sorger et al., 2007). PS does not have any difficulty in recognizing visual objects: she does not complain of any object recognition problems, she was perfect and fast at recognizing the colorized Snodgrass and Vanderwart stimuli (Rossion & Pourtois, 2004). PS performed in the normal range at discriminating nonface objects in previous studies. Rossion et al. (2003) showed that PS was able to discriminate objects from two homogeneous categories: cars and novel objects ("scott objects", available here: http://tarrlab.cnbc.cmu.edu///stimuli.html). Schiltz et al. (2006) proposed another task requiring exemplars discrimination of five categories: birds, boats, cars, chairs and faces. While PS was strongly impaired for face category, she performed in the normal range for the four nonface categories. PS' visual field is almost full (with exception of a small left paracentral scotoma, as in many cases of acquired prosopagnosia following right posterior ventral lesions, see Bouvier & Engel, 2006), her visual acuity is good (0.8 for both eyes as tested in August 2003), and despite the right hemisphere lesion encompassing area V4/V8, her color perception is in the lower normal range (see Sorger et al., 2007).Finally, although this is not the focus of the present study, it is also important to note that recent studies carried out with the patient PS have strongly suggested that her impairment is related to an inability to process individual faces holistically. That is, she does not show any inversion effect (Busigny & Rossion, in press), and no whole-part advantage or composite face effects (Ramon et al., 2010), which are clear markers of holistic face processing (e.g., Maurer, Le Grand, & Mondloch, 2002; Tanaka & Farah, 1993; Young, Hellawell, & Hay, 1987). PS' eye gaze fixations during face recognition are also focused on local facial features – particularly the mouth – rather than in between features, suggesting an analytical strategy for face individualization (Orban de Xivry, Ramon, Lefèvre, & Rossion, 2008).For the present study, PS was tested in the two first experiments in 2005, aged 55, and in the third one in 2008, aged 58.

3. General methodological considerations

In all experiments, we used an ABX presentation mode, in order to avoid response biases, which could potentially be observed in same/different or old/new recognition tasks in brain-damaged patients (e.g., Gauthier et al., 1999). Hence, participants were usually presented with a first stimulus followed by two simultaneously presented stimuli (unlimited duration) side by side, and they had to choose the correct one among the pair corresponding to the previously presented target. Accuracy rates and correct RTs were measured, and participants were instructed to try to be as accurate as possible, and to press response keys as soon as they believe to have an answer.

For each experiment we tested a group of sex- and age-matched controls, with no history of neurological or vascular disease, head injury or alcohol abuse, and without cognitive complaints. All participants signed a consent form explaining the general goal of the experiment. The data of age-matched control participants are displayed as individual data in illustrations rather than as averages to be able to identify abnormal response patterns of patients with respect to all normal controls tested.

For statistical comparisons of the results of the patients to the control participants, rather than using *Z*-scores, we used a modified T-test developed specifically for single-case studies (Crawford & Howell, 1998). This procedure decreases 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 for the patient.

4. Experiments

4.1. Novel 3D geonlike shapes

4.1.1. Rationale

Our initial systematic investigation of the issue of visual homogeneity with PS started with simple 3D *geonlike* (Biederman, 1987) shapes. This experiment provided a relatively objective way to manipulate the degree of visual similarity between a target item to recognize and discriminate from a distractor, by selecting distractors increasing in visual similarity compared to the target by the kind and number of 3D transformation that were performed. The sensitivity of the paradigm was tested first in a group of age-matched control participants, measuring their accuracy and RTs at seven levels of similarity between the target and the distractor. The conditions were ranked according to their level of difficulty (increasing) based on a pilot experiment performed with 10 younger controls (undergraduate students). According to the visual homogeneity view of prosopagnosia, the increase in accuracy and correct RTs should be steeper for PS as compared to normal observers.

4.1.2. Methods

4.1.2.1. Participants. Seven sex- and age-matched participants were tested (age range: 49–56).

4.1.2.2. Stimuli. Twelve simple 3D *geonlike* object shapes were generated in 3D Studio Max. Each base shape could be slightly transformed according to three independent parameters (bent/taper/size). Seven different conditions were created, varying in the kind of dimensions that were manipulated and their numbers. Hence, the stimuli could vary in one dimension only [3 conditions: Bent (1B), Size (1S), Taper (1T)], two dimensions [3 conditions: Bent/Size (2BS), Bent/Taper (2BT), Size/Taper (2ST)], or the three dimensions altogether [1 condition: Bent/Size/Taper (3BST)]

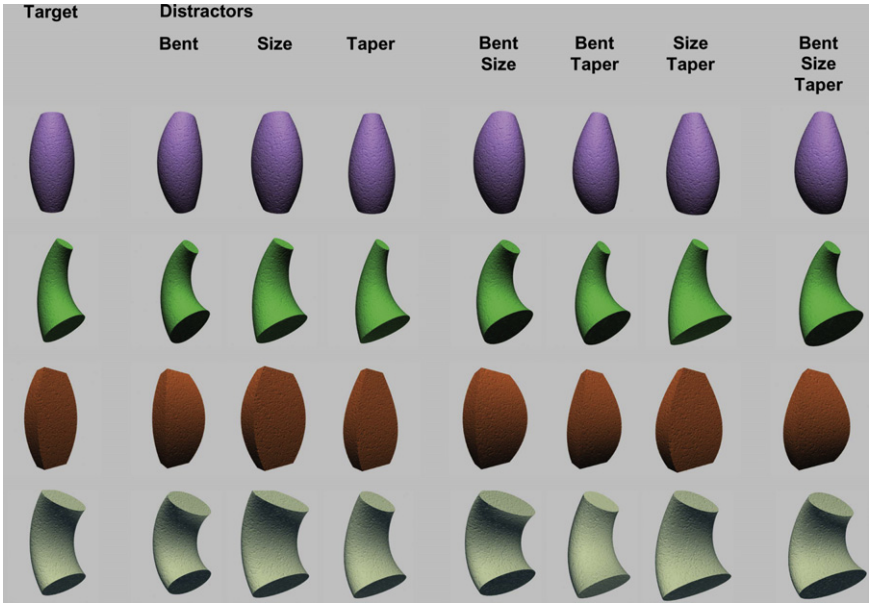

Fig. 1. Examples of stimuli used in experiment 1 (Novel 3D geonlike shapes) with the 7 levels of modification.

(Fig. 1). The stimuli sustained were also variable in size, depending on the geon base shape, with minimal/maximal values of roughly 1.5°/5° width and 3°/6° height of visual angle, at 40 cm from the monitor.

4.1.2.3. Procedure and analysis. The participants were presented with a 2-alternative forced-choice (2AFC) matching task. A first stimulus was presented in the centre of the screen for 500 ms, followed after 500 ms of blank screen by a pair of stimuli remaining on the screen until the participant's response. Stimuli size was quite variable, depending on the shape used. One of the items of the pair was a distractor, and the other one was the same as the target, but the two items of the pair were slightly rotated in depth (10° clockwise or counter-clockwise). The distractor could differ from the target either by one dimension, two dimensions, or three dimensions. Thus, there were 7 levels of analysis: Bent or Taper or Size (1 dimension); Bent/Size, Bent/Taper, Size/Taper (2 dimensions); Bent/Size/Taper (3 dimensions). There were 48 trials for each of the conditions, giving 336 trials (4 blocks of 84 trials). Trial order was fully randomized. The left and right positions of the target

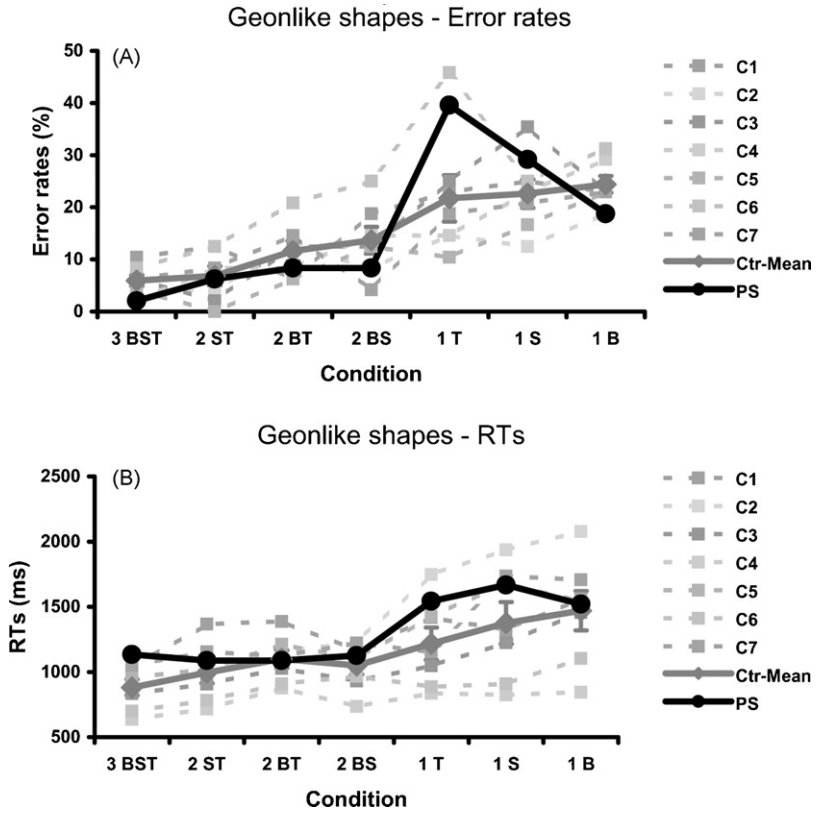

Fig. 2. (A) Error rates of PS and control participants in experiment 1, for the 7 conditions: Bent/Size/Taper (3BST), Size/Taper (2ST), Bent/Taper (2BT), Bent/Size (2BS), Taper (1T), Size (1S), and Bent (1B). Bars represent the standard errors. (B) Correct response times of PS and control participants in experiment 1. Bars represent the standard errors.

Table 2
PS' accuracy rates and response times for the experiment 1: Discrimination of gradually similar Geonlike shapes. Legend: Bent/Size/Taper (3BST), Size/Taper (2ST), Bent/Taper (2BT), Bent/Size (2BS), Taper (1T), Size (1S), and Bent (1B).

A

	Error rates (%)				RTs (ms)			
	Controls	PS	*T*	*p* (one-tailed)	Controls	PS	*T*	*p* (one-tailed)
3 BST	5.95	2.08	1.293	*0.12*	881	1134	−1.452	*0.10*
2 ST	6.85	6.25	0.114	*0.46*	996	1087	−0.383	*0.36*
2 BT	11.61	8.33	0.588	*0.29*	1099	1087	0.063	*0.48*
2 BS	13.69	8.33	0.738	*0.24*	1050	1126	−0.395	*0.35*
1 T	21.73	39.58	−1.417	*0.10*	1216	1543	−0.927	*0.20*
1 S	22.62	29.17	−0.844	*0.22*	1376	1667	−0.640	*0.27*
1 B	24.40	18.75	1.232	*0.13*	1470	1520	−0.117	*0.46*
Overall	15.26	16.07	0.162	*0.44*	1155	1309	−0.583	*0.29*

B

	Error rates (%)				RTs (ms)			
	Controls	PS	*T*	*p* (one-tailed)	Controls	PS	*T*	*p* (one-tailed)
3 BST	5.95	2.08	1.293	*0.12*	881	1072	−1.096	*0.16*
2 ST	6.85	10.42	−0.679	*0.26*	996	1269	−1.150	*0.15*
2 BT	11.61	4.17	1.333	*0.12*	1099	1293	−1.019	*0.17*
2 BS	13.69	4.17	1.312	*0.12*	1050	1306	−1.330	*0.12*
1 T	21.73	27.08	−0.425	*0.34*	1216	1425	−0.592	*0.29*
1 S	22.62	25.00	−0.307	*0.39*	1376	1279	0.213	*0.42*
1 B	24.40	25.00	−0.131	*0.45*	1470	1413	0.133	*0.45*
Overall	15.26	13.99	0.254	*0.40*	1155	1294	−0.526	*0.31*

(A) PS' first performance. (B) PS' second performance.

stimuli were counterbalanced across test items and participants received no feedback for their responses. Error rates and RTs for correct responses were analyzed.

4.1.3. Results

For the group of normal age-matched controls, the ANOVA showed significant differences between conditions in error rates ($F_{6,24} = 15.179$, $p < 0.001$). The linear contrast was highly significant ($F_{1,6} = 105.9$, $p < 0.001$), reflecting the linear increase of error rates (slope 3.08% errors/step) with the degree of visual similarity between the target and the distractor (Fig. 2A). The analysis of variance showed also a significant effect of visual similarity in correct RTs ($F_{6,24} = 11.468$, $p < 0.001$). The linear contrast analysis showed a significant linear increase of RTs with visual similarity of the distractor and the target ($F_{1,6} = 17.6$, $p < 0.01$) (Fig. 2B). The slope was 98.12 ms/step.

At the easiest level of discrimination (baseline), PS could not be distinguished from the group of normal controls neither for error rates (PS: 2.08%; mean: 5.95%; $t = 1.293$, $p = 0.12$), nor for correct response times (PS: 1134 ms; mean: 881 ms; $t = 1.452$, $p = 0.10$) (Table 2A). Overall, PS' error rates were no different than the controls (PS: 16.07%; mean: 15.26%; $t = 0.162$, $p = 0.44$) and she was as fast as them (PS: 1309 ms; mean: 1155 ms; $t = 0.583$, $p = 0.29$). For each condition (level) considered separately, PS' error rates were in the normal range (Fig. 2A; Table 2A) and she was as fast as the controls (Fig. 2B). Her performance was slightly less accurate in the condition "Taper" (1T), but one control participant (C6) was even less accurate than her in this condition (45.83% of errors) and PS was not significantly impaired in comparison with the controls group ($t = 1.417$, $p = 0.10$) (Table 2A). Yet, to ensure that her rather low performance in the difficult "taper only" condition did not reflect an abnormal score, we performed two additional controls. First, PS was tested the next day with the same experiment. Her results were virtually identical to the first time she performed the experiment, with overall error rates decreasing only mildly (2.08%) and RTs being virtually identical (15 ms faster overall, i.e. about 1% of decrease) (Table 2B; Supplementary Figure I). However, and importantly, her performance was much better this time in the "taper only" condition (27.08% of errors; RTs: 1425 ms), and no different at all from the controls' performance ($p = 0.34$ for error rates; $p = 0.29$ for RTs). Finally, we performed an additional test of PS most recently (February 2010) with the "taper only" trials (96 trials), about 4 years after the initial testing. PS' performance was quite good in this difficult condition (81/96; RTs: 1765 ms). One gender- and age-matched control performing the same experiment obtained a score of 83/96 with an average response time of 1715 ms.

With respect to the initial set of data collected, PS shows the same profile that the control group concerning the differences between conditions, both for error rates ($F_{6,335} = 7.555$, $p < 0.001$) and correct RTs ($F_{6,261} = 4.543$, $p < 0.001$). PS also obtained a significant slope dependant of the level of similarity in accuracy ($p < 0.001$) and in correct RTs ($p < 0.001$). For error rates, PS' slope (2.78/step) was in the normal range (controls' mean: 3.08; $t = 0.334$, $p = 0.38$). For RTs, PS' slope (64.33/step) was also in the normal range (controls' mean: 98.12; $t = 0.673$, $p = 0.26$).

4.1.4. Discussion

This first experiment showed that PS does not present with any impairment in discriminating novel 3D *geonlike* shapes that differ either by one, two or three manipulations (bent, size and taper). She is as accurate and as fast as the control group for each level of difficulty, i.e. similarity between the target and its distractor. The increasing slope of her error rates and RTs with increasing levels of visual similarity was identical for the patient and the control participants. This pattern of result does not support the general visual similarity hypothesis of prosopagnosia, for which a steeper slope should have been observed for the prosopagnosic patient compared to the controls.

4.2. Common objects

4.2.1. Rationale

The goal of the second experiment was to assess more precisely the visual similarity hypothesis by means of a set of common multiparts objects. Two-D images of common objects were used and morphed along a continuum. This morphing provided an objec-

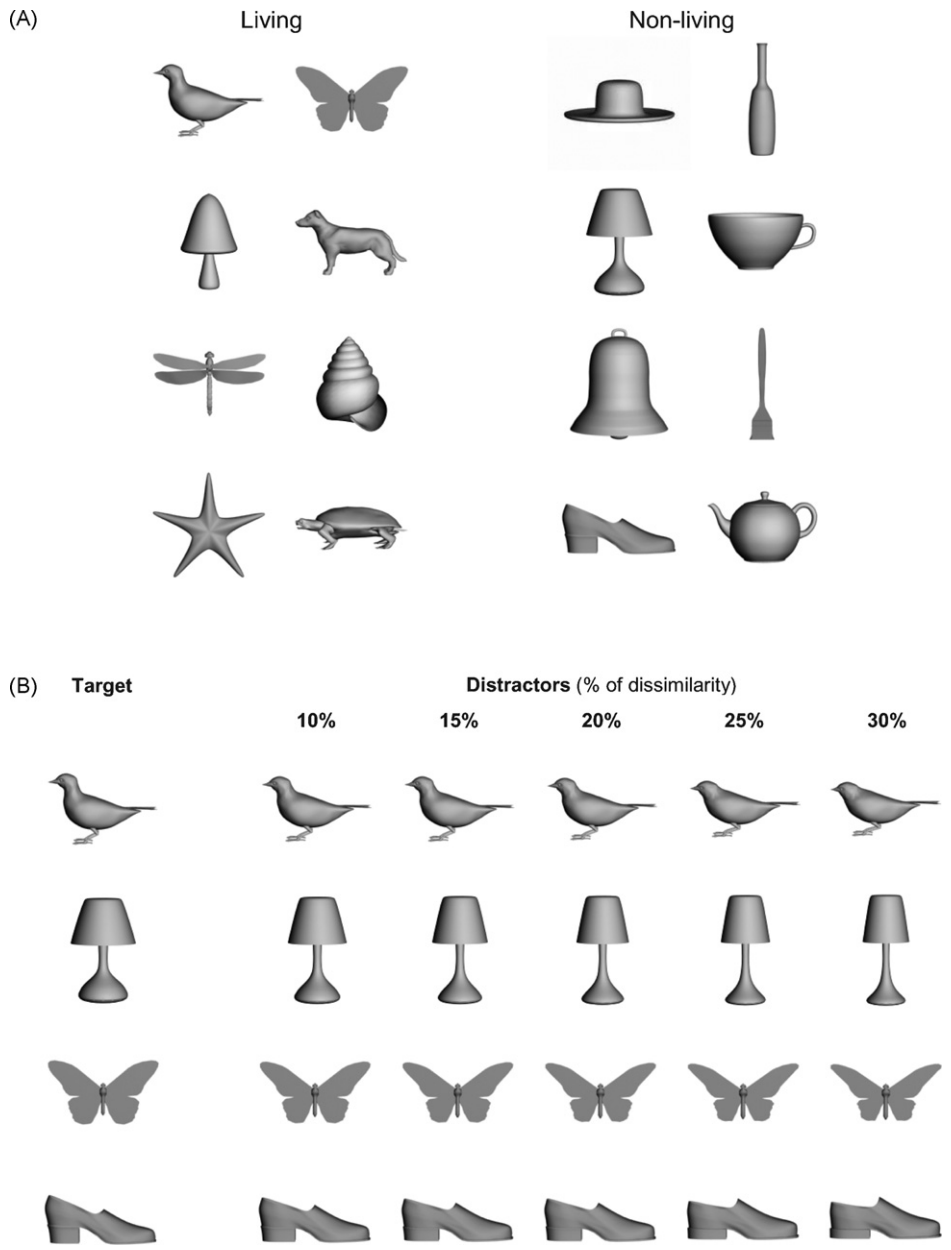

Fig. 3. (A) Stimuli used in experiment 2 (common objects). (B) Examples of morphed pairs in experiment 2, following the 5 levels of dissimilarity.

tive way to manipulate the degree of visual similarity between the target item to recognize and discriminate from a distractor, by selecting distractors which were at increasing distances from the target on the morph continuum.

4.2.2. Methods

4.2.2.1. Participants. Seven sex- and age-matched participants, including five who performed the previous experiments, were tested (age range: 49–56).

4.2.2.2. Stimuli. The stimuli were made from a set of common object pictures developed by Graf and colleagues (Hahn, Close, & Graf, 2009), which could be morphed in pairs to create intermediate object shapes (Fig. 3A). We used sixteen categories of common objects, including 8 living (bird, butterfly, dog, dragon fly, mushroom, snail, starfish, turtle) and 8 non-living objects (bell, bottle, cup, hat, lamp, paintbrush, pot, shoe) (Fig. 3A). For each category, two exemplars were created as 3-D models, differing in shape (e.g. a wide and a thin lamp), using 3ds max^{TM} 4.2 (Discreet, Montreal, Canada). These two morph parents were constructed so that they had the same number of vertices, and corresponding object parts were defined by corresponding vertices. Morphing the shape of one object into another shifts the vertex points from their initial positions in 3-D space along linear trajectories towards the positions of the corresponding vertices. Thus, the two morph parents constituted the extremes of a continuum. On each continuum, morphed pictures between these two exemplars were created every 5%, from 1% to 100%. Thus, for each original target (1%) we obtained 20 distractors of increasing dissimilarity (5% = very similar; 100% = very dissimilar). We conducted a pilot testing with the full continuum, in order to make the task sufficiently difficult and sensitive to increasing steps (5%) of visual similarity. In the end, we selected, for each target (1%), 5 levels of distractors on the morph continuum: 10%, 15%, 20%, 25% and 30% (Fig. 3B). The stimuli were quite variable in size, depending on the category, with minimal/maximal values of roughly 1.5°/5° width and 3°/6° height of visual angle, at 40 cm from the monitor.

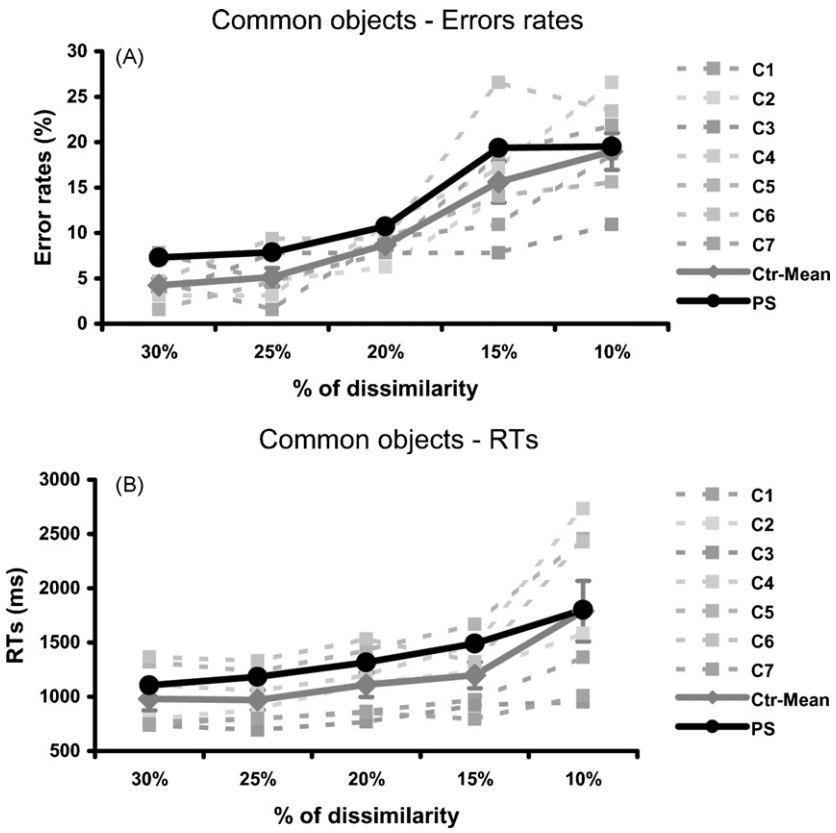

Fig. 4. (A) Error rates of PS and control participants in experiment 2, for each level of dissimilarity between the target and distractor items. Bars represent the standard errors. (B) Correct response times of PS and control participants in experiment 2. Bars represent the standard errors.

4.2.2.3. Procedure and analysis. The participants were presented with a 2-alternative forced-choice (2AFC) matching task. A first stimulus was presented in the centre of the screen for 500 ms, followed after 750 ms of blank screen by a pair of stimuli remaining on the screen until the subject's response. One of the items of the pair was the same as the first one, and the other one was a distractor. The distractor could differ from the target by 10%, 15%, 20%, 25% or 30% along the continua (Fig. 3B). The target was always an extreme point of the continuum (1% or 30%), such that participants could not anticipate the difficulty of discrimination (i.e. if the target was a 20%, they could have anticipated a very difficult discrimination). There were 64 trials for each of the 5 conditions (4 trials for each of the 16 pairs). This gave 320 trials in total (4 blocks of 80 trials). Trial order was fully randomized. The left and right positions of the target stimuli were counterbalanced across test items and participants received no feedback for their responses. Error rates and RTs for correct responses were analyzed.

4.2.3. Results

Regarding error rates, the ANOVA for the control group showed significant differences between conditions ($F_{4,24} = 25.375$, $p < 0.001$). The linear contrast was highly significant ($F_{1,6} = 49.96$, $p < 0.001$), reflecting the linear increase of error rates with the degree of visual similarity between the target and the distractor. The slope was 3.68 errors/5% similarity (Fig. 4A). The analysis of correct RTs confirmed this pattern of results, showing a significant effect of visual similarity in correct RTs ($F_{4,24} = 14.183$, $p < 0.001$) and a significant linear contrast ($F_{1,6} = 18.983$, $p < 0.01$). The average slope was 202 ms/5% similarity (Fig. 4B).

At the easiest level of discrimination (baseline), PS' error rate could not be distinguished from the control participants (PS: 7.29%; mean: 4.24%; $t = 1.456$, $p = 0.10$). Her correct RTs were also within normal range (PS: 1107 ms; mean: 980 ms; $t = 0.423$, $p = 0.34$) (Table 3). When considering all conditions altogether, PS' data were also completely in the normal range in error rates (PS: 12.95%; mean: 10.54%; $t = 0.891$, $p = 0.20$) and correct response times (PS:

Table 3
PS' accuracy rates and response times for the experiment 2: Discrimination of gradually similar common objects.

	Error rates (%)				RTs (ms)			
	Controls	PS	*T*	*p* (one-tailed)	Controls	PS	*T*	*p* (one-tailed)
30%	4.24	7.29	−1.456	*0.10*	980	1107	−0.423	*0.34*
25%	5.13	7.87	−0.964	*0.19*	970	1184	−0.831	*0.22*
20%	8.71	10.71	−1.231	*0.13*	1111	1317	−0.649	*0.27*
15%	15.63	19.35	−0.575	*0.29*	1199	1491	−0.856	*0.21*
10%	18.97	19.51	−0.094	*0.46*	1790	1803	−0.016	*0.49*
Overall	10.54	12.95	−0.891	*0.20*	1210	1380	−0.442	*0.34*

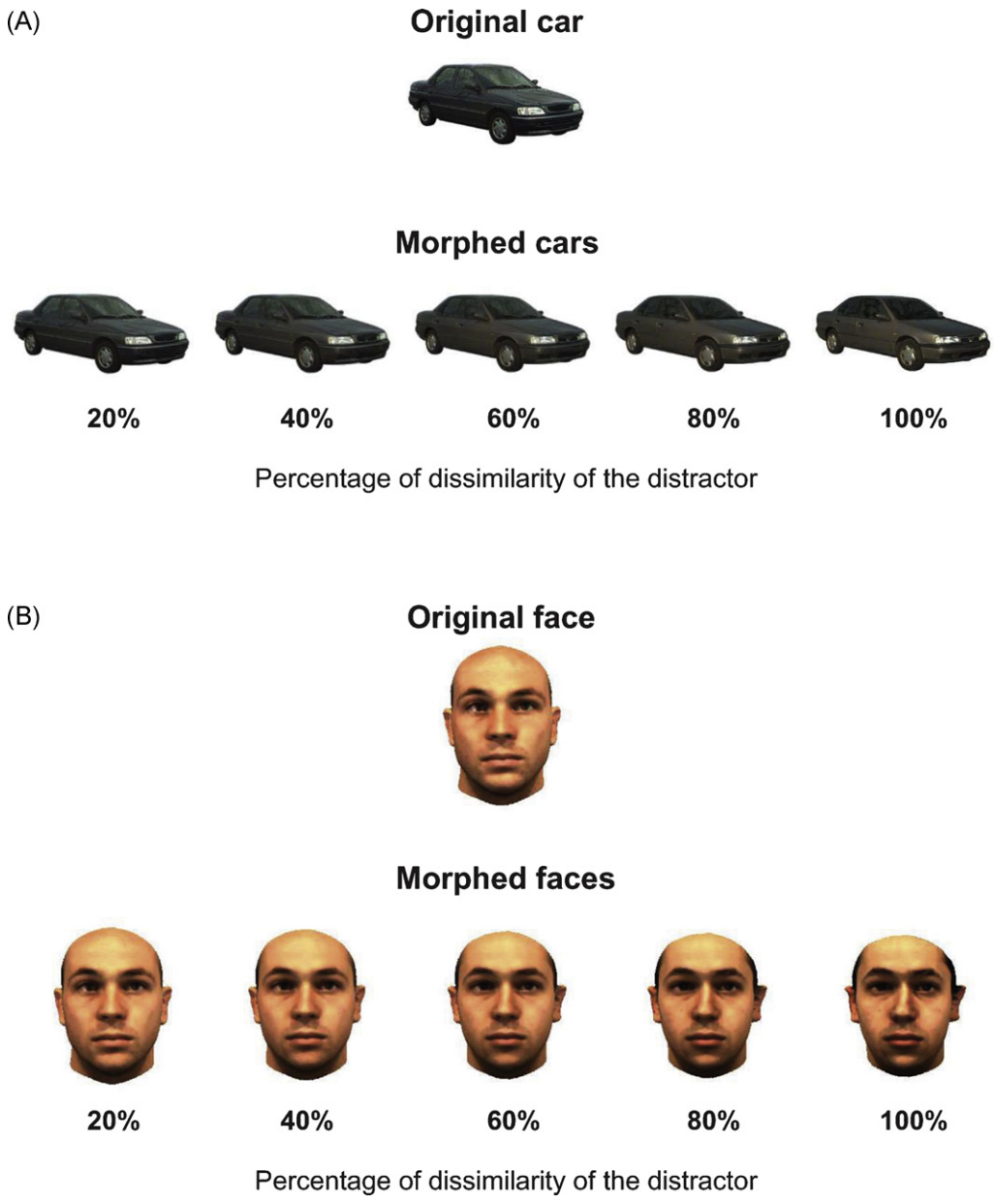

Fig. 5. Examples of stimuli used in experiment 3, following the 5 levels of dissimilarity. (A) Car condition. (B) Face condition.

1380 ms; mean: 1210 ms; $t = 0.442$, $p = 0.34$) (Table 3). Interestingly, there was no difference between living and non-living objects, PS and controls performing at he same level for both classes of stimuli: the succeeded items were equally spread in the two lasses for the control participants (non-living: 51%, living: 49%), as well as for PS (non-living: 52%; living: 48%).

PS data (error rates and RTs) were not different from the controls at any of the similarity levels considered separately (Table 3), and, critically, error rates and correct RTs did not show a steeper increase over the 5 levels of visual similarity (Fig. 4A and B), as would be predicted by the visual similarity hypothesis. That is, PS shows the same profile of performance as the control participants concerning the differences between conditions. The ANOVA on her data showed significant differences between conditions in error rates ($F_{4,319} = 2{,}369$, $p < 0.05$) and correct RTs ($F_{4,279} = 8.689$, $p < 0.001$). PS obtained also a significant slope dependant of the level of similarity in accuracy ($p < 0.01$) and in correct RTs ($p < 0.001$). For error rates, PS' slope (3.06/5%) was in the normal range (controls' mean: 3.68; $t = 0.457$, $p = 0.33$). For RTs, PS' slope (174/5%) was also in the normal range (controls' mean: 202; $t = 0.208$, $p = 0.42$).

4.2.4. Discussion

In summary, there was a linear increase of error rates and RTs for normal aged-matched control participants, showing that the manipulation was effective in these participants. The results show that PS was at the same level than the control group at each level of difficulty/similarity, both in error rates and response times. Most importantly for our purpose, the patient's pattern of responses was strictly identical to normal observers, the slope of increased error rates and RTs with degrees of visual similarity being identical to normal participants. Overall, this pattern of results argues, again, against the visual similarity view that acquired prosopagnosic patients would show a steeper increase of error rates and/or RTs with increasing levels of visual similarity between the items to discriminate (Gauthier et al., 1999).

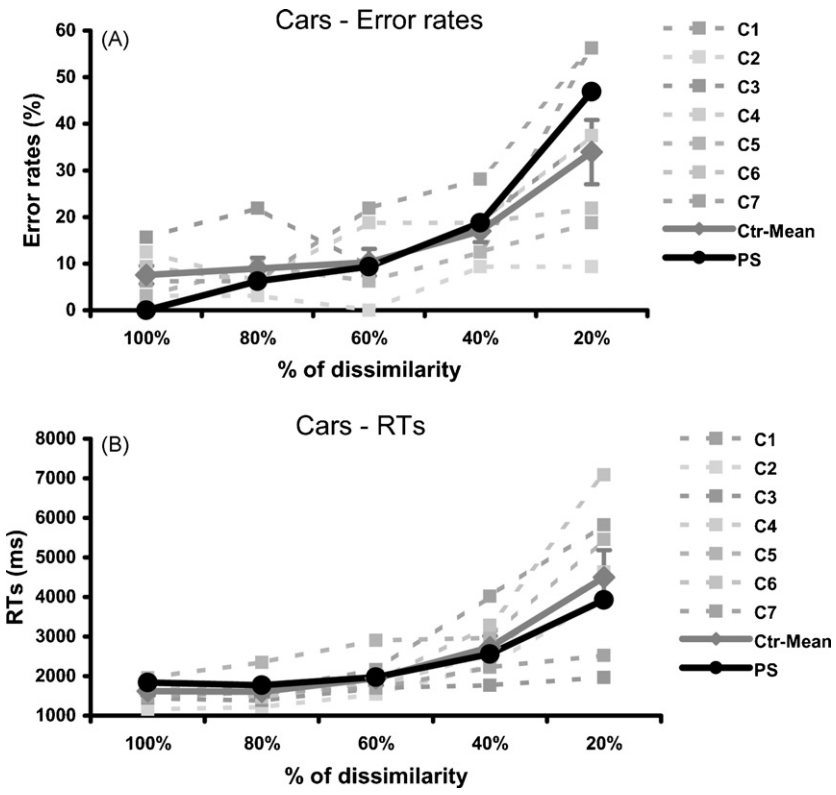

Fig. 6. (A) Error rates of PS and control participants in experiment 3 (car condition), for each level of dissimilarity between the target and distractor items. Bars represent the standard errors. (B) Correct response times of PS and control participants in experiment 3 (car condition). Bars represent the standard errors.

4.3. Homogen cars and faces

4.3.1. Rationale

This last experiment was conducted to test further the sensitivity to visual similarity in the case of PS, this time with real photographs, and using parametric manipulations of visual similarity within the same category of stimuli. Here we used pictures of cars, a highly familiar nonface object category often contrasted with faces (see e.g., Rossion, Collins, Goffaux, & Curran, 2007 for the use of the same stimuli), that we manipulated by 2D morphing (Morph^{TM}). The other goal of this experiment was to compare PS' discrimination abilities for nonface familiar objects (cars) and faces, for which we also manipulated the levels of similarity parametrically.

A prediction of the visual similarity account of acquired prosopagnosia is that the prosopagnosic patients will have relatively more difficulties at discriminating 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 to discriminate are extremely similar. However, if their impairment is not due to general difficulties to discriminate visually similar items, they should not present with an exaggerated decrease of performance when similarity increases, with both cars and faces. Therefore, we expect that prosopagnosic patients should be preserved at discriminating photographs of cars at all levels of visual similarity. In contrast, if their impairment reflects damaged processes that are specialized for face stimuli, we expect that they should be impaired with faces at all levels of visual similarity, even when faces to discriminate are extremely different (i.e., very easy for controls).

4.3.2. Methods

4.3.2.1. Participants. This experiment was performed three years after the two previous ones. Thus, we selected seven new sex- and age-matched controls (age range: 53–63).

4.3.2.2. Stimuli. Twenty photographs of cars were selected and were morphed two-by-two with Morph^{TM}. We extracted 5 distractors in increasing order of dissimilarity from each original car photograph (20, 40, 60, 80 and 100%) (Fig. 5A). For faces, thirty-two color laser scanned pictures of faces (from the Max-Planck Institute, Germany) were used (half female) and were morphed two-by-two (Morphable Model For The Synthesis Of 3D Faces; Blanz & Vetter, 1999). As for pictures of cars, we used 5 levels of (dis)similarity for the distractors (20, 40, 60, 80 and 100%) (Fig. 5B). Overall, we used 32 trials for each level. The cars stimuli sub-

Table 4
PS' accuracy rates and response times for the experiment 3: Discrimination of gradually similar cars.

	Error rates (%)				RTs (ms)			
	Controls	PS	*T*	*p* (one-tailed)	Controls	PS	*T*	*p* (one-tailed)
100%	7.59	0.00	1.403	*0.11*	1617	1834	−0.741	*0.24*
80%	8.93	6.25	0.411	*0.35*	1607	1766	−0.413	*0.35*
60%	10.27	9.38	0.111	*0.46*	1946	1975	−0.058	*0.48*
40%	16.96	18.75	−0.270	*0.40*	2731	2554	0.219	*0.42*
20%	33.93	46.88	−0.663	*0.27*	4496	3925	0.293	*0.39*
Overall	15.54	16.25	−0.102	*0.46*	2369	2255	0.187	*0.43*

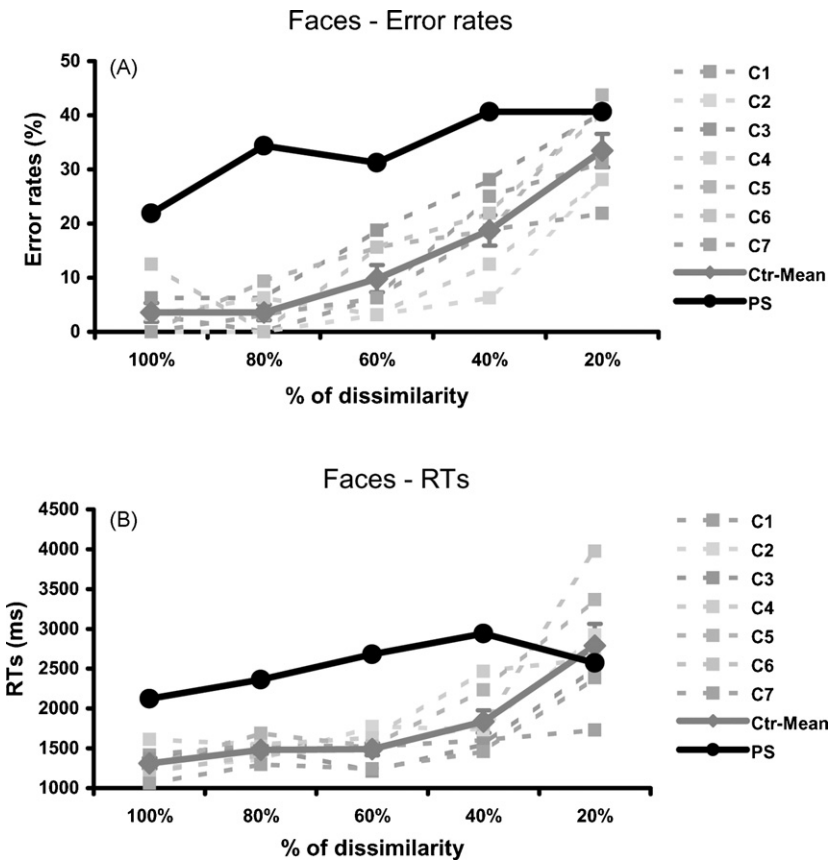

Fig. 7. (A) Error rates of PS and control participants in experiment 3 (face condition), for each level of dissimilarity between the target and distractor items. Bars represent the standard errors. (B) Correct response times of PS and control participants in experiment 3 (face condition). Bars represent the standard errors.

tended approximately 5.7° × 12.7° and the faces stimuli 7.8° × 6.4°, at 40 cm from the monitor. They were displayed on a white background.

4.3.2.3. Procedure and analyses. The participants were presented with a 2-alternative forced-choice (2AFC) matching task. The target was presented first during 2000 ms, followed by an ISI (1000 ms) and then a screen appeared showing the target accompanied with one distractor. This distractor consisted in one of the five levels of morphing of the target item. The participants had to decide which of the two probe pictures was the same than the previous one by pressing a corresponding key. The experiment was divided into four blocks of 80 trials (blocks 1 and 3 displayed faces and blocks 2 and 4 displayed cars, and the order was kept identical for each control and the patient). Participants were expected to perform better and faster with the most dissimilar distractor, with a progressive increase of error rates and RTs as the visual similarity between the target and distractor increases. If visual similarity accounts for the face processing impairment of PS, then the slope of increase of error rates and correct RTs should be steeper for PS than for normal controls.

4.3.3. Results

4.3.3.1. Pictures of cars. In error rates, there were significant differences between conditions for the control group ($F_{4,24} = 11.874$, $p < 0.001$). The linear contrast was highly significant ($F_{1,6} = 16.282$, $p < 0.01$), reflecting the linear increase of error rates with the degree of visual similarity between the target and the distractor. The slope was 6.58 errors/20% similarity (Fig. 6A). The analysis of correct RTs confirmed this pattern of results, showing a significant effect of visual similarity ($F_{4,24} = 17.673$, $p < 0.001$) and a significant linear contrast ($F_{1,6} = 21.774$, $p < 0.01$). The average slope was 720 ms/20% similarity (Fig. 6B).

At the easiest level of discrimination (baseline), PS made no mistake (mean: 7.59%; $t = 1.403$, $p = 0.11$) and she was as fast as the control participants (PS: 1834 ms; mean: 1617 ms; $t = 0.741$, $p = 0.24$) (Table 4). Overall, her error rate was in the normal range (PS: 16.25%; mean: 15.54%; $t = 0.102$, $p = 0.46$) and she was as fast as control participants (PS: 2255 ms; mean: 2369 ms; $t = 0.187$, $p = 0.43$). Moreover, PS' error rates and response times were in the normal range for each level of dissimilarity (Table 4). Most importantly, PS' error rates did not show a steeper increase over the 5 levels of visual similarity than control participants (Fig. 6A and B). For PS, there were significant differences between conditions in error rates ($F_{4,159} = 9.639$, $p < 0.001$) and correct RTs ($F_{4,126} = 21.101$, $p < 0.001$) and the linear contrast was also significant for both measures ($ps < 0.001$). For error rates, PS' slope (11.72/20%) was in the normal range (control's mean: 6.58; $t = 1.052$, $p = 0.17$). For RTs, PS' slope (523/20%) was also in the normal range (control's mean: 720; $t = 0.444$, $p = 0.34$).

4.3.3.2. Pictures of faces. With faces, there was also a significant increase of error rates with levels of similarity in the control group ($F_{4,24} = 50.146$, $p < 0.001$). The linear contrast was highly significant ($F_{1,6} = 155.07$, $p < 0.001$), reflecting the linear increase of error rates with the degree of visual similarity between the target and the distractor. The slope was 7.48 errors/20% similarity (Fig. 7A). For correct RTs, there was also a significant effect of visual similarity in correct RTs ($F_{4,24} = 19.297$, $p < 0.001$) and a significant linear contrast ($F_{1,6} = 26.512$, $p < 0.01$). The average slope was 369 ms/20% similarity (Fig. 7B).

Table 5
PS' accuracy rates and response times for the experiment 3: Discrimination of gradually similar faces.

	Error rates (%)				RTs (ms)			
	Controls	PS	*T*	*p* (one-tailed)	Controls	PS	*T*	*p* (one-tailed)
100%	3.57	21.88	−3.746	*0.00***	1312	2121	−4.324	*0.00***
80%	3.57	34.38	−7.582	*0.00***	1481	2362	−6.243	*0.00***
60%	9.82	31.25	−3.033	*0.01**	1489	2682	−5.580	*0.00***
40%	18.75	40.63	−2.750	*0.02**	1835	2942	−2.754	*0.02**
20%	33.48	40.63	−0.814	*0.22*	2788	2573	0.277	*0.40*
Overall	13.84	33.75	−3.921	*0.00***	1707	2516	−4.135	*0.00***

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

With faces, PS' performance looked quite different than her own performance in all previous experiments with nonface stimuli, and than control participants' performance. At the easiest level of discrimination (baseline), PS was strongly impaired, making more than 20% of errors (PS: 21.88%; mean: 3.57%; $t = 3.746$, $p < 0.01$). She was also significantly slowed down relative to control participants (PS: 2121 ms; mean: 1312 ms; $t = 4.324$, $p < 0.01$) (Table 5; Fig. 7A and B). Overall, PS also made many more mistakes than the controls (PS: 33.75%; mean: 13.84%; $t = 3.921$, $p < 0.01$) although she performed clearly above chance level ($Chi^2 = 16.9$, $p < 0.001$). PS was also generally significantly slower than the controls (PS: 2516 ms; mean: 1707 ms; $t = 4.135$, $p < 0.01$). If we consider each level separately, it is clear that PS was impaired both in accuracy and correct RTs for the four first levels (100% to 40%). However, her performance was not worse than the controls for the most difficult (i.e. similar) level (20%) in error rates (PS: 40.63%; mean: 33.48%; $t = 0.814$, $p = 0.22$) and in correct RTs (PS: 2573 ms; mean: 2788 ms; $t = 0.277$, $p = 0.40$) (Table 5).

Regarding the slopes of error rates and RT increases, PS showed a slightly different pattern than with nonface items. There was no significant difference between conditions in error rates ($F_{4,159} = 0.858$, $p = 0.25$) and correct RTs ($F_{4,98} = 1.697$, $p = 0.08$) (Fig. 7A and B). The linear contrast analysis on error rates showed a marginally significant effect only ($p = 0.051$), and the analyses of RTs showed a significant slope ($p < 0.05$). Because PS was already impaired at the easiest discrimination level, her error rates and RTs' slopes appeared slightly different than those of the control participants, yet they were in the normal range (Error rates: PS: 4.69; mean: 7.48; $t = 1.450$, $p = 0.10$; RTs: PS: 113; mean: 369; $t = 1.203$, $p = 0.14$).

4.3.4. Discussion

As expected, the control participants showed significant increases with the degree of similarity between a target and its distractor: the more similar the distractor was to the target the more their performance decreased. This was the case both for car and face stimuli. For photographs of cars, PS showed exactly the same profile of response as the controls. However, for faces, she presented a quite different profile of performance. She was already well below normal performance at the easiest level of dissimilarity, and consequently, her performance slope was somewhat flatter than the control participants' performance. Once again, these observations go clearly against the view that acquired prosopagnosia is associated with increasing difficulty at discriminating visually similar items. In fact, for individual face discrimination, it is when the target and the distractor differ substantially that the impairment of the patient is the most clearly visible.

5. General discussion

Following three behavioral experiments performed with a well-defined case of prosopagnosia following brain damage (PS), we report strong evidence that, at least for this patient, acquired prosopagnosia cannot be accounted for by a more general visual impairment at individualizing visually similar shapes or objects, contrary to an old and still influential view (Blanc-Garin, 1984; Damasio et al., 1982; Faust, 1955; Gauthier et al., 1999). The first experiment shows that PS is capable of processing 3D novel shapes as well as normal controls. Increasing the level of similarity between a target and a distractor item (by reducing the number of simple stimulus transformations between the target and distractor) increased error rates and correct RTs to the same extent for normal controls and the patient. The second experiment demonstrates that PS can discriminate living and non-living pictures of multi-parts objects, and she again showed a linear increase of performance with increasing levels of visual similarity between target and distractor that was identical to normal controls. These observations were also made in experiment 3 when parametric manipulation of similarity was done within a visually homogenous familiar category (cars). Altogether, these results do not only show that PS is able to discriminate visually similar objects as well as normal observers, but that she shows the same sensitivity to manipulations of visual similarity. Finally, the results obtained with face stimuli in the third experiment are particularly interesting because they show that PS is impaired and slowed down at individual face discrimination even when this discrimination is easy for normal controls. Moreover, her error rates and RTs increased similarly, or if anything even less steeply than normal controls with increases of visual similarity (because of her performance being already lower at the easiest levels of discrimination), an observation which counters completely the visual similarity hypothesis.

5.1. No strong evidence supporting the visual similarity account of prosopagnosia

In the introduction, we suggested that the most influential alternative hypothesis against face-specificity of prosopagnosia could be defined as the "*general categorization within a visually homogenous category*" hypothesis. This view was explicitly formulated mainly by Damasio et al. (1982), and later by Gauthier et al. (1999). We believe that, in comparison to these previous studies, we offered here a much more stringent test of this hypothesis with the prosopagnosic patient PS. However, our observations led us to directly contradict this view. First, we tested this hypothesis here with a patient who does not present any impairment at basic-level object recognition, contrary to the cases of general visual agnosia described by Damasio et al. (1982) and those tested by Gauthier et al. (1999). We believe that if one aims at challenging the face-specificity view of prosopagnosia, it is important to test patients who, like PS and a few others reported in the neuropsychological literature (see Table 1), do not already present with important object recognition impairments in simple neuropsychological tests. Admittedly, our data do not contradict the possibility that brain-damaged patients with general visual agnosia, as tested by Gauthier et al. (1999), may have indeed relatively larger difficulties (error

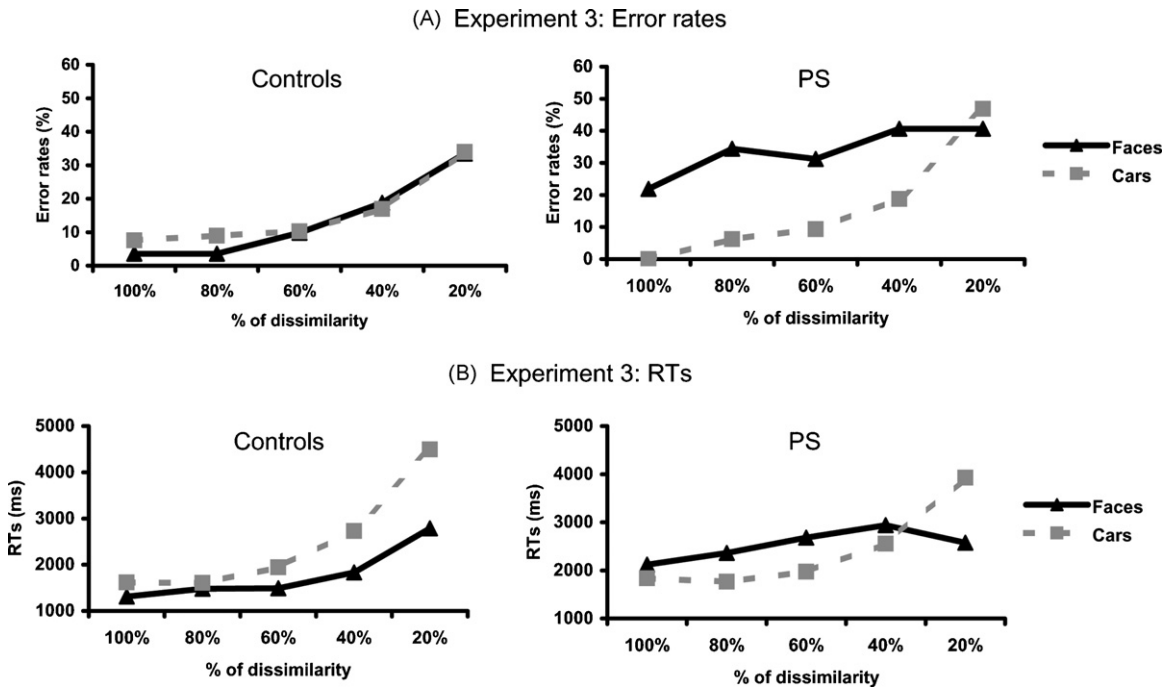

Fig. 8. Comparison of performance for cars *vs.* faces in experiment 3, for PS compared to the group of normal controls. (A) Error rates. (B) Correct RTs.

rates and RTs) with increasing levels of visual similarity for objects (and faces) than normal observers. However, considering our own observations, we argue that such effects obtained in visual agnosic patients are not directly relevant for the issue of face-specificity of prosopagnosia. Moreover, a careful look at the experiments and data reported by Gauthier et al. (1999) in several experiments casts doubts about these authors' claim of particularly large impairments for their patients relative to controls with increasing visual similarity, even for their cases of general visual agnosia. As mentioned in the introduction, one limitation of that study was that the degree of visual similarity between a target and its distractor did not increase objectively (as done here in experiments 2 and 3 at least), i.e. parametrically. Consequently, controls did not even show systematic and linear decreases of performance with increasing levels of similarity in several experiments of Gauthier et al. (1999), making difficult to interpret patients' performance. Another issue is that in most experiments of that study but the first one, patients' performance does not really appear to decrease significantly more than the controls with increasing levels of similarity, especially if one takes into account baseline differences between the patients and the normal observers. Here, we did not have this baseline issue (the patient performing as well as controls for the most dissimilar items, except for faces in experiment 3), and we tested this alternative hypothesis of prosopagnosia with a parametric manipulation of object (and face) similarity, leading to clear linear decreases of performance in normal observers. Thus, to our knowledge, the present study is the first to report a stringent test of the hypothesis that increasing visual similarity in discrimination would cause particular difficulties for prosopagnosic patients, leading to a rejection of that hypothesis. Such experiments could potentially be used to test cases of more general visual agnosia, in order to clarify whether their difficulties in object recognition is related to some extent to visual similarity.

To summarize, based on the present study and a careful look at previous studies, we believe that there is no empirical evidence to date supporting the view that prosopagnosia can be explained by a defect at distinguishing among visually similar items, i.e. at subordinate-level visual categorization. Rather the present study provides a strong case against this view.

5.2. PS, one of few cases of pure face agnosia

The present observations reinforce our claim that the patient PS, following her brain-damage, presents with a selective impairment at recognizing faces (Busigny & Rossion, in press; Rossion et al., 2003; Schiltz et al., 2006). We do not claim that PS is the first patient to present with such pure face agnosia impairment, but we believe that among the few such cases that have been reported in the literature (listed in Table 1), she has been tested the most stringently for her visual object processing abilities.

In the introduction, we highlighted five issues to consider for studies aiming at assessing the face-specificity of the deficit in prosopagnosia. We would like to confront our own study, and previous evidence collected with the patient PS, to these issues.

(1) We mentioned that one cannot be certain that a prosopagnosic patient would be able to recognize all visually complex objects. Of course, this issue is also present in the case of PS: we cannot claim that she would recognize all nonface objects since we can test only a limited set of items. However, across three previous studies (Busigny & Rossion, in press; Rossion et al., 2003; Schiltz et al., 2006) and in the present experiments, PS never scored below normal range when having to recognize/discriminate nonface objects, and she was tested with common drawings of objects (colorized Snodgrass and Vanderwart by Rossion & Pourtois, 2004), novel shapes (single parts and multi-parts objects), models and photographs of common living and non-living objects, and individual items from several visual categories. Consequently, we believe that PS' recognition disorder is truly specific for face category.

(2) We also emphasized the importance of using tasks of equal difficulty for faces and nonface objects. In fact, here we did not equalize the level of performance in the third experiment between car and face conditions for normal controls. Indeed, controls performed slightly better with faces than cars at the easiest levels of discrimination, and they were consistently faster for faces than for cars (Fig. 8A and B). Thus, discriminating pictures of individual cars

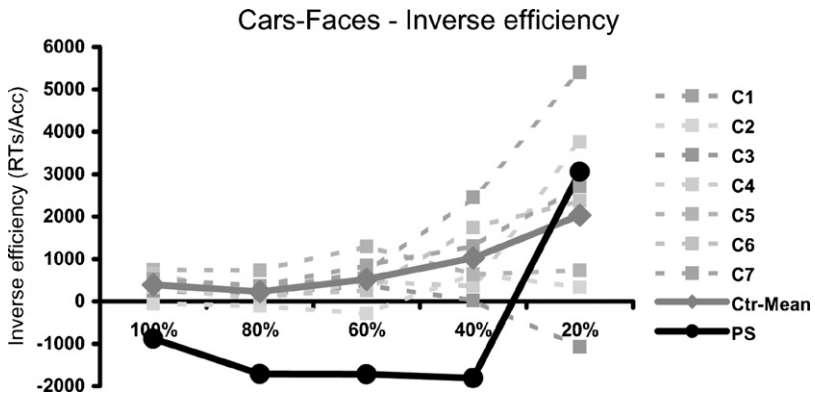

Fig. 9. Comparison of performance for cars *vs.* faces in experiment 3, for each participant. The data are expressed in inverse efficiency (correct RTs divided by accuracy rates) to take into account the two measures and potential speed-accuracy trade-offs. Positive values mean that faces are better performed than cars.

in our experiment was slightly more difficult than discriminating pictures of faces. If anything, this difference even reinforces our point, since PS, despite this inherent larger difficulty for cars than faces for normal controls, performs much better with photographs of cars than with faces (both in error rates and correct RTs, Fig. 8A and B). Strikingly, when considering both accuracy rates and RTs in a combined measure of efficiency (average response times of the correct trials divided by accuracy; Townsend & Ashby, 1983), she appears to be the only participant to present with this profile of response (Fig. 9). This reinforces the claim that PS is severely impaired at processing individual faces, but that she still has all the abilities to process other homogeneous nonface objects, even if they are more difficult to discriminate than faces. We note also that PS, unlike some previously tested cases of prosopagnosia (Barton, Hanif, & Ashraf, 2009; Sergent & Signoret, 1992), does not have any particular interest or expertise in makes of cars.

(3) and (4) We also suggested in the introduction that even prosopagnosic patients with no other visual recognition impairment may appear to have slightly more troubles than normal controls in object processing tasks, due to associated defects (i.e., low-level visions, selective attention, memory, . . .) that have nothing to do with their visual recognition impairment. One must thus be careful not to overinterpret any lower performance of a prosopagnosic patient compared directly to normal controls in a given object processing task. For instance, it is remarkable that PS, despite extensive lesions concerning part of her visual system, can perform tasks of object discrimination and recognition at a normal level of performance. Nevertheless, one should keep in mind that she has a small left paracentral scotoma, her visual acuity is slightly below normal range (8/10), her color perception is in the normal but lower range as well (see all details in Sorger et al., 2007), and she was slightly slower than normal controls in a phasic alert task performed a few years ago (Rossion et al., 2003).

Hence, even though she was as fast as normal controls in the present experiments, she may occasionally present with a significant slowdown in object matching tasks when compared to normal participants who do not present low-level vision impairments (Busigny & Rossion, in press; Rossion et al., 2003; see also De Haan et al., 1995 for clear evidence that such impairments do not account or even contribute to the face recognition difficulties in prosopagnosia). However, her error rates are never larger than controls for objects (contrary to faces), and these relative response times increases are not consistent and do not appear to be related to any particular object category, the presentation mode, or the change of viewpoint between target and probe item (Busigny & Rossion, in press; Rossion et al., 2003; Schiltz et al., 2006; the present study). In any case, the present data show that PS is completely able to respond efficiently and rapidly in tasks of nonface object discrimination, even with highly visually similar items. Giving these results and thus the lack of support for the alternative view of prosopagnosia, and even if we completely agree with Gauthier et al. (1999) that correct RTs are important to consider when judging a patient's performance at a given task, we would attribute the rare slowdown of PS in some object processing tasks to such low-level visual impairments, and perhaps to the patient – being fully aware of these additional difficulties – being sometimes particularly conservative in taking her decision.

(5) Finally, Riddoch et al. (2008) recently suggested that prosopagnosic patients could obtain normal performance in object processing tasks if they only had to match physically identical pictures, and that this could not be taken as evidence for preserved object recognition. While this is certainly valid point, we argue that it is not a critical in judging object processing abilities in cases of prosopagnosia. First, when cases of visual agnosia are tested with identical images of objects at encoding and recognition, they still show massive impairments (e.g., Delvenne, Seron, Coyette, & Rossion, 2004; Gauthier et al., 1999), contrary to cases of pure prosopagnosia. Second, patients with prosopagnosia like PS show massive impairments in face matching tasks, whether the exact same image is presented at encoding and recognition (experiment 3), or even when having to match simultaneously presented faces (e.g., patient NS in Delvenne et al., 2004). If such a compensatory strategy would be at play for objects, there is no reason to expect that it could not be used for faces. Third, and in any case, regarding the patient PS, there is evidence that she can match and recognize pictures of objects presented under different viewpoints (e.g., experiment 1 here, experiment 3 in Busigny & Rossion, in press).

Since the best alternative hypothesis against face-specificity does not hold, one has to acknowledge that, at least in some cases, acquired prosopagnosia may concern only the category of faces. The case of PS, with a large body of data provided across several studies, provides perhaps the strongest case to date for face-specific agnosia.

5.3. The specificity of impairments in face recognition: functional implications

Observing patients with brain-damage who present such a selective impairment for processing individual faces raises an important issue. That is, it is often stated that the very existence of an agnosia specific to faces is evidence that faces are handled by a modular system (e.g., Kanwisher, 2000), especially if there are also rare cases who show the inverse dissociation (object agnosia without prosopagnosia, Moscovitch, Winocur, & Behrmann, 1997). However, the fact that there are recognition impairments restricted to faces does not necessarily imply that

faces are handled by a system which processes only this kind of stimuli (i.e., a domain-specific system, or module, Coltheart, 1999). There are processes that presumably developed through experience to deal efficiently with faces, just because these stimuli pose particular challenges for the visual recognition system: faces are indeed highly similar, they are made of multiple (internal) parts, their differences cannot be verbalized easily, we need to individualize them, they undergo fast (expression) and slow (ageing) changes, etc. In the adult visual recognition system, this process or set of processes – most likely the ability to process individual items holistically/configurally – may not be modular, in the sense that it (they) may *potentially* be recruited also for object recognition to a certain extent (e.g., for instance an area of the right middle fusiform gyrus responds preferentially but not exclusively to faces, e.g. Kanwisher, McDermott, & Chun, 1997). However, what the evidence of cases of pure prosopagnosia indicates is that while these processes are strictly *necessary* for being efficient at face recognition, they are not necessary for object recognition. Thus, following brain damage, in particular in the ventral visual stream of the right hemisphere, object recognition may be preserved while face recognition may be impaired. Despite important debates about this issue, 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. Evidence for and against this view has been found so far. Against the expertise view, prosopagnosic patient RM in Sergent & Signoret (1992) could recognize cars better than experts and patient WJ could recognize sheep faces but not human faces (McNeil & Warrington, 1993). Moreover, the visual agnosic patient CK could not recognize well known planes and toy soldiers despite his normal face recognition (Moscovitch et al., 1997). In contrast, support for the expertise view comes from the finding that 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, Bornstein, Sroka, & Munitz, 1969; Assal, Favre, & Anderes, 1984; fish in a fisherman and a fish salesman, Takahashi, Kawamura, Hirayama, Shiota, & Isono, 1995; Clarke, Lindemann, Maeder, Borruat, & Assal, 1997; plants in a florist, Clarke et al., 1997; mountains in an alpinist, Clarke et al., 1997).

Evidence regarding the visual expertise account of prosopagnosia is thus mixed. The point we want to make here is that, as Meadows (1974) put it early on, there is no necessary discrepancy between the observation of isolated defects at face recognition and a visual expertise account which would considers the face recognition system as being flexible rather than modular (Tarr & Gauthier, 2000): *"We learn to distinguish faces to a degree not seen with other categories because facial recognition is from the very earliest age and throughout life such an essential and determining aspect of daily living. Thus, it can be argued that we might have acquired the same perceptual skill in relation to the configuration of one tree relative to the next, if tree configuration were as major a determinant of behaviour as is faces. [. . .] Facial recognition becomes by far the most complex and frequently encountered example of relatively pure visual discrimination learning that occurs in everyday life. Considered in this way it becomes less surprising that it may be disturbed in relative isolation*" (Meadows, 1974, p.490).

6. Conclusions

In three delayed matching experiments in which visual similarity between the target and a distractor was manipulated parametrically, we demonstrated that the brain damaged prosopagnosic patient PS was able to discriminate objects from visually homogenous categories: novel 3D geometric shapes manipulated on single or multiple dimensions, morphed common objects, and morphed photographs of a highly homogenous familiar category (cars). In all experiments, the prosopagnosic patient showed normal performance and speed, and there was no evidence of a steeper increase of error rates and RTs with increasing levels of visual similarity. These data rule out an account of acquired prosopagnosia in terms of a more general impairment in discriminating objects from visually homogenous categories. Rather, it seems that brain damage in adulthood may lead to selective recognition impairment for faces, perhaps the only category of visual stimuli for which holistic/configural perception is required to individualize members of the category.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.neuropsychologia.2010.03.026.

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