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Research report

Impaired processing of relative distances between features and of the eye region in acquired prosopagnosia—Two sides of the same holistic coin?

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ABSTRACT

Acquired prosopagnosia (AP) is characterized by impaired recognition of individual faces following brain damage. The nature of the functional impairment(s) underlying AP remains debated. Recent studies have demonstrated deficient processing of diagnostic information in the region of the eyes (Caldara et al., 2005); other studies suggest that patients fail to judge relative distances between facial features (Barton et al., 2002). We hypothesized that these apparently different observations are related to a common cause. More precisely, we suggest that AP arises due to an impairment of a process that reduces uncertainty about the nature/location of the diagnostic cues for face individualization: the ability to perceive multiple elements of a face as a single global representation (holistic processing). Being impaired at processing individual faces holistically, prosopagnosic patients would tend to perform relatively worse for processing facial areas containing multiple elements (i.e., the eyes), and for elements that are widely spaced apart. Here we tested PS, a single case of AP, at matching unfamiliar faces differing either with respect to local features or inter-feature distances, over the upper and lower areas of the face. A pilot study and Experiment 1 confirmed that PS was extremely poor at using information encompassing the eyes, but was also deficient at perceiving relative distances between features. When uncertainty about the location and nature of the diagnostic cue was removed in Experiment 2, PS' performance remained below normal range, but she improved substantially. Most interestingly, her pattern of performance across the different conditions appeared qualitatively identical to that of normal controls. In line with previous observations of PS and other cases of prosopagnosia, our findings indicate that the reduced reliance on the area of the eyes and on relative distances between features in AP may have a common underlying cause—the disruption of holistic processing of the individual face.

1. Introduction

Normal face processing involves adequate perception of different cues that are thought to be diagnostic for face individualization. For instance local shape (Young et al., 1985) and surface (color/texture) (Lee and Perrett, 1997; Russell et al., 2006) information can be derived for this purpose, with the region of the eyes/eyebrows conveying particularly critical

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sources of information (Haig, 1985; Gosselin and Schyns, 2001; Sadr et al., 2003).

The high efficiency with which we generally perceive and recognize faces masks a complexity which becomes apparent when this ability breaks down, as observed in acquired prosopagnosia (AP) (Bodamer, 1947). This rare neurological condition refers to the selective inability to recognize individual faces as a consequence of brain damage to bilateral or right unilateral occipito–temporal regions. Since the first observations (Wigan, 1844; Quaglino et al., 2003; for recent reviews see Barton, 2003; Mayer and Rossion, 2007) the clinical and anatomical conditions of AP have attained considerable notoriety as they provide a means to clarify the neuro-functional mechanisms of normal face processing.

However, despite over 60 years of research on AP, the underlying functional basis of the observable deficits in deriving an adequate representation of an individual face remains a matter of debate.

It has been proposed that AP involves a deficit in processing the face as a global representation, i.e., configural/holistic processing.[1] For instance, based on their assessment of LH, Levine and Calvanio (1989) concluded that prosopagnosia represents a loss of visual ''configural processing'', which they conceptualized 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*'' (p. 151). This view has been supported by other studies of acquired prosopagnosic patients that used different paradigms to test the interdependence between facial features of the whole face (e.g., Sergent and Villemure, 1989; Saumier et al., 2001; Boutsen and Humphreys, 2002). However, the different paradigms used and the variability among patients tested has hindered true significant progress with respect to validation of this hypothesis and thus of our understanding of the nature of this configural/holistic processing view of AP. Furthermore, the fact that different authors conceptualize configural/holistic processing differently (e.g., Farah et al., 1998; Maurer et al., 2002), poses additional problems.

More recent studies indicate that prosopagnosia involves a deficit restricted to the processing of certain localized features of the face. Caldara et al. (2005) tested the acquired prosopagnosic patient PS (Rossion et al., 2003) by means of a learning paradigm followed by an identification task of faces revealed through random apertures (''Bubbles'', Gosselin and Schyns, 2001). Compared to normal observers, PS required much more information to achieve the same performance level and relied mostly on the mouth rather than on the eyes. In the same vein, Bukach et al. (2006) showed that the prosopagnosic patient LR was able to detect diagnostic changes in the mouth region, but was strikingly impaired at making such judgments based on the eyes of faces (see also Bukach et al., 2008; Rossion et al., 2009).

Also recently, other authors have reported several patients who were impaired at discriminating faces that differed with respect to distances between features (e.g., mouth-nose distance, inter-ocular distance, ...) but could apparently process local features (e.g., eye color) efficiently (Barton et al., 2002; Joubert et al., 2003; Barton and Cherkasova, 2005). Barton et al. (2002) therefore concluded that the perception of the relative distances between features of faces is impaired in patients with prosopagnosia, in particular when their lesions involve the right fusiform gyrus, and that this deficit contributes directly to their prosopagnosia.

These last two hypotheses differ from the proposed holistic/configural hypothesis of AP described above. They suggest that prosopagnosia arises from the inability to process a certain *type* of information—local information conveyed by the eyes (Caldara et al., 2005; Bukach et al., 2006) or the relative distances between facial features in general (Barton et al., 2002)—rather than from an impaired mode of processing (i.e., holistic, as opposed to analytical).

One the one hand, it is tempting to attribute these different observations to the functional variability among acquired prosopagnosic patients (Sergent and Signoret, 1992; Schweich and Bruyer, 1993), and to acknowledge that the main impairment observed in prosopagnosia—the inability to process faces at the individual level efficiently—has several different manifestations, which would presumably rely on the specific localization of a patient's lesion(s). On the other hand, another way to conceptualize these observations is to integrate all of them into a single theoretical framework. That is, while acknowledging the functional variability among prosopagnosic patients in terms of associated deficits, it may be that all of these patients share a common disrupted process, which characterizes their prosopagnosia.

In line with previous studies and our interpretation of the observations made for the patient PS, we hypothesized that the primary *cause* of AP lies in the inability to process faces holistically/configurally. More precisely, all patients suffering from AP would be unable (or significantly less able) to ''*integrate the multiple features of an individual face simultaneously, into a unified perceptual representation*'' (Tanaka and Farah, 1993; Rossion, 2008a). Consequently, they would have to process a face feature-by-feature, analytically, or over a small spatial window at a time. Since the region of the eyes contains several elements (two eyes and two eyebrows, at least), a disruption of the ability to process these elements as a whole would be particularly detrimental for the diagnosticity of this facial region. In the same vein, processing a distance between features requires the processing of at least two elements over a wider spatial range than processing a localized single feature. Hence, the loss of the ability to process both the eye region of the face (Caldara et al., 2005; Bukach et al., 2006; Rossion et al., 2009) and the relative distances between features (Barton et al., 2002; Barton and Cherkasova, 2005) may not reflect distinct fundamental aspects of AP, but rather represent mere *consequences* of a single cause: a defective holistic processing mode.

[1] These terms have been used interchangeably in the face processing literature, even though a number of authors have used the term ''configural'' to refer specifically to the processing of relative distances between features that would be diagnostic of someone's identity (e.g., Rhodes, 1988; Carey, 1992; Maurer et al., 2002). Here we will use the term ''holistic'' or ''configural'' to refer to a process, not to specific cues of the stimulus. In line with earlier proposals (Farah et al., 1998), this process can be defined as the ''*ability to perceive the multiple elements of a(n) (upright) face simultaneously, as an integrated representation*'' (Rossion, 2008a, 2008b). Its empirical manifestation is characterized by the interdependence between facial features.

This view would have the advantage of accounting for the above outlined observations within a single theoretical framework. However, it remains quite speculative at this stage. One way to provide support for this hypothesis would be to demonstrate that (1) the same patients present difficulties in processing the area of the eyes and relative distances between features, and (2) that these two phenomena can be directly related to a disruption of the ability to process the face holistically.

With respect to (1), we recently noted that in addition to their impairment at detecting eye changes in a delayed matching task, both PS' and LR's performance at detecting mouth changes was correct but slow relative to controls when the modification concerned the mouth-nose distance, but not the size of the mouth (Rossion et al., 2009). Hence, the patients may indeed exhibit a particular defect at both processing information at the level of the eye region, and of relative distances between features. In an exploratory investigation of PS' ability to discriminate relative distances between features we also noted a pattern of performance which supported a defect in processing relative distances between features. This experiment required same/different judgments of face stimuli that had been used in a study with normal observers (Goffaux and Rossion, 2007; see Fig. 1a). PS completed four blocks of 20 trials/condition, presenting a quite poor performance overall, but with large differences in performance between the perception of inter-feature distances and judgments which could be done locally: nose/mouth changes > eye changes > eye-nose distance > inter-ocular distance (unpublished data, Fig. 1b and c). Her performance for local feature

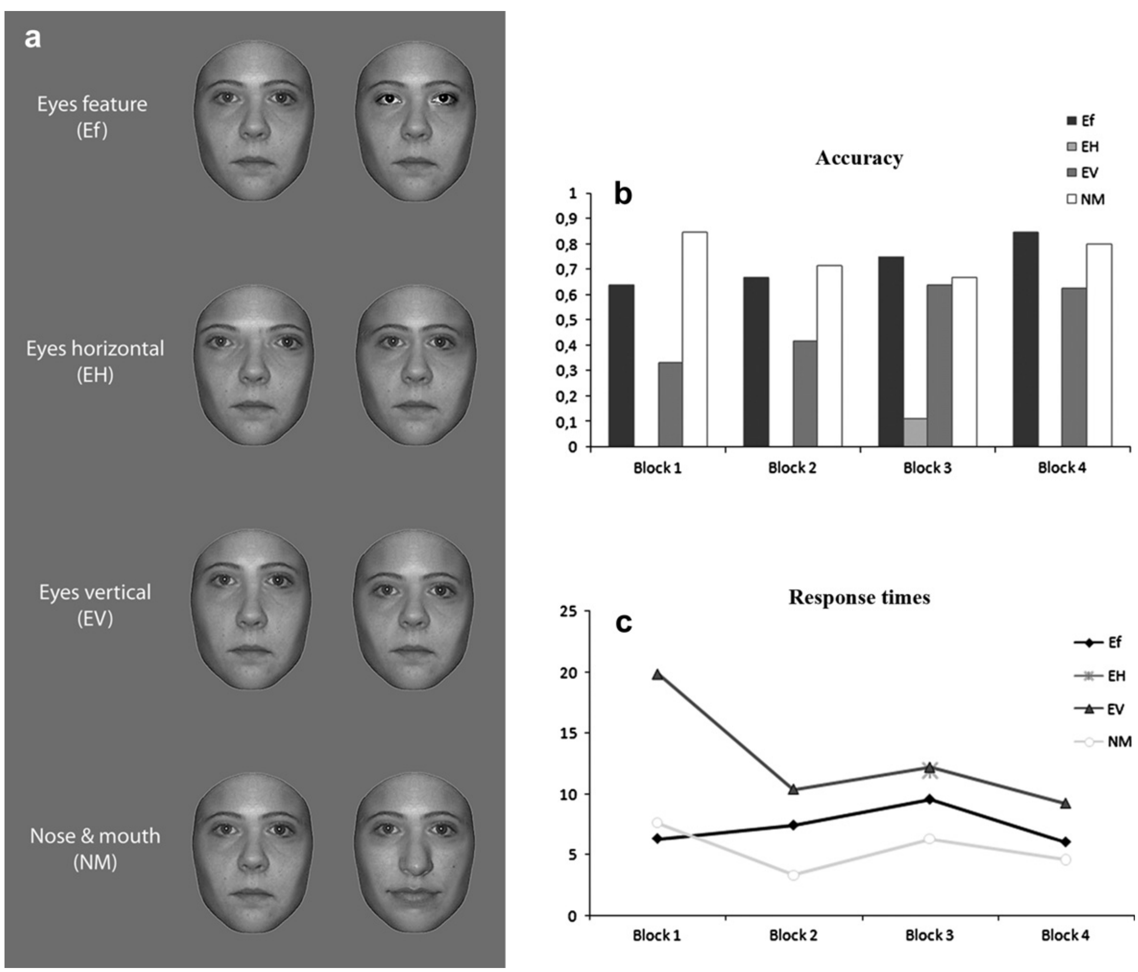

Fig. 1 – Exploratory investigation of face discrimination for the patient PS. a. Examples of the stimuli used in an initial same-different experiment with two faces presented side-by-side. Four conditions (equalized for difficulty in normal observers) were used to test PS' ability to discern relative distances between features (inter-ocular distance, EH; eyes–nose distance, EV), as well as featural information (eyes only, Ef; nose/mouth NM), respectively. The stimuli used were identical as those employed by Goffaux and Rossion (2007); conditions were presented at random with unlimited time to respond. b–c. PS' accuracy and RTs (in sec) for "different" trials are displayed as a function of (consecutive) testing sessions (84 trials per block, half of which required a "different" response). PS' performance reflected a strong feature versus relative distance dissociation: for single and combined feature changes (Ef, NM) she was reasonably above chance, contrary to her extremely poor performance at judging relative distances, for which she generally displayed a strong bias for "same" responses (with lower performance for EH as compared to EV; only for block 3 did she detect any differences for EH). Note that performance varied across sessions: her initially high performance for NM decreased as it increased progressively for Ef and EV changes.

changes (eyes, and nose/mouth) was reasonably above chance, which was in sharp contrast to her extremely poor performance at judging relative distances between these features. Thus, we had preliminary evidence that the patient PS was also impaired at processing relative distances between features. However, we noted that her performance for the different conditions changed across blocks, increasing for some conditions (e.g., vertical distances between features), but apparently at the expense of other conditions (Fig. 1). Moreover, it turned out that during extra sessions, PS verbally stated having suddenly realized the type of manipulation she had been repeatedly missing previously—the inter-ocular distance. Thereafter, PS' performance improved dramatically for this condition, even reaching perfect scores, albeit with extremely prolonged RTs.

Thus, even though PS did not automatically perceive the differences in relative distances between features, she was able to successfully discriminate them once she was aware of the modifications employed. This anecdotal observation seems in line with behavior of other prosopagnosic patients as reported in the literature. Patients 3 and 4 reported by Barton et al. (2002) "*did markedly better*" when required to discriminate relative distances in blocks of "mouth only trials". Furthermore, when given unlimited time to discriminate faces, their performance also increased substantially. Similarly, Joubert et al. (2003) reported markedly improved performance when their patient FG, who presented with prosopagnosia following a degenerative disease extending to the fusiform gyrus, was made aware of the nature and location of the cues for discriminating faces (eyes color, mouth–nose distance, inter-ocular distance). Finally, Bukach et al. (2006) found that performance of their patient, LR, "*improves substantially if eye trials are blocked*"—specifically, the condition for which his performance was well below normal level when trials were presented randomly.

To summarize, several cases of AP appear to perform poorly at discriminating relative distances as well modifications of the eyes, but can improve substantially if made aware of the nature and location of the diagnostic cues on the face (including the eyes and the relative distance between features). This suggests that the primary cause of their difficulties in processing individual faces may be the disruption of the ability to process all the diagnostic features of a face at once, in a single representation, i.e., their deficit may be an impairment of holistic face processing.

1.1. *Goals and hypotheses of the present study*

The goal of the present study was to provide support for this view by testing the prosopagnosic patient PS' ability to discriminate individual faces based on features and relative inter-feature distances, in two different situations. Given the observations above, the rationale of our investigation was as follows. For a normal observer who has to discriminate between individual faces, an intact holistic processor is *functional* because any diagnostic cue (e.g., a change in the shape of the mouth, or inter-ocular distance) affects the perception of other (more or less distally located) features of the whole face (Tanaka and Farah, 1993; Tanaka and Sengco, 1997). Hence, if two faces differ only in terms of one element (the shape of one feature), the ability to process faces holistically allows rapid identification of the source and location of the information diagnostic for face individuation. In other words, for the normal observer "*The general expression of a face is the sum of a multitude of small details, which are viewed in such rapid succession that we seem to perceive them all at a single glance. If any one of them disagrees with the recollected traits of a known face, the eye is quick at observing it, and it dwells upon the difference. One small discordance overweighs a multitude of similarities and suggests a general unlikeness*" (Galton, 1883). However, for the prosopagnosic patient who, presumably, has abnormal holistic processing, facial cues would be perceived one at a time. Thus, a sequential search among many different cues encompassing the entire face would be necessary in order to identify the diagnostic cue. If this notion were correct, indicating the nature of the cue diagnostic for face discrimination should not only improve the patient's performance, but furthermore his/her *profile* of response should become more similar to that of normal observers. Consequently, the relatively larger impairment for processing information at the level of the eyes and of distances between features in AP should be cancelled out, or at least strongly reduced.

Here we tested this hypothesis with the patient PS, a case of AP following lesions to the right inferior occipital cortex and left middle fusiform gyrus, who has been reported in detail in previous studies (e.g., Rossion et al., 2003; Caldara et al., 2005; Schiltz et al., 2006; Sorger et al., 2007).

PS was tested with an individual face matching task in which we manipulated the kind of internal facial cue diagnostic for discrimination (vertical change at the level of the eyes or mouth, inter-ocular distance, featural changes of the mouth, nose or eyes). The two experiments reported in the following differed only with respect to potential a priori knowledge of changes to be discriminated (uncertainty: random trial presentation, *vs* certainty: trials blocked by condition with participants informed about the nature of the cue). Our main hypothesis was that the region-dependent processing deficit reported previously for PS (observed for the eyes) would disappear if she was informed about change location/type to be discriminated and most importantly that, overall, she would present a response profile similar to that of normal observers under this condition.

2. Methods

2.1. *Participants*

2.1.1. *The patient PS*

Since detailed functional and anatomical descriptions of the patient PS can be found elsewhere (Rossion et al., 2003; Caldara et al., 2005; Schiltz et al., 2006; Sorger et al., 2007), we will only briefly summarize her clinical history and functional deficits. PS is a 59 year-old (born in 1950) right-handed woman who works as a kindergarten teacher. She sustained closed head injury in 1992. Structural scanning revealed extensive lesions of the left mid-ventral (mainly fusiform gyrus) and the right inferior occipital cortex. Medical treatment and neuropsychological rehabilitation promoted her recovery (Mayer and Rossion, 2007), leaving only a profound prosopagnosia as a remainder of her initially pronounced cognitive deficits. She has a general difficulty at recognizing faces, including those of family members as well as her own, and relies on contextual or suboptimal facial cues (Caldara et al., 2005) to determine a person's identity. The Benton Facial Recognition Test (Benton and Van Allen, 1972) ranks her as highly impaired (score: 27/54, as tested shortly after her accident; 38/54 within over 37 min as tested in 2007) and the Warrington Recognition Memory Test (WRMT; Warrington, 1984) for faces characterizes her as significantly less accurate than controls (score: 18/25). She does not present any difficulty in recognizing objects, even at a subordinate level, as reflected by her normal accuracy scores and RTs for within-category discriminations of highly similar non-face objects (Rossion et al., 2003; Schiltz et al., 2006). PS' visual field is almost full (small left paracentral scotoma), and her visual acuity is good (.8 for both eyes as tested in August 2003). The performance of PS on standard clinical and neuropsychological tests of visual perception and recognition is summarized elsewhere (Sorger et al., 2007, Table 1).

2.1.2. *Control participants*

Apart from PS, ten undergraduate students (aged 19–21) from the department of Psychology (University of Louvain, Belgium) who received course credit for participation, as well as two age-matched controls (mean age = 52) participated in both experiments.

2.2. Stimuli

Using FACES™ 3.0 (InterQuest™, 1998), we created eight grayscale, unfamiliar, schematic base faces (see Fig. 2a). Importantly, the stimuli lacked textural and contour information, which may have likely aided PS' increase in performance in our exploratory experiments. Our aim was to create a situation in which strategic use of such information (e.g., comparing the distance from one eye to the contour for changes of the horizontal eye position) was the least possible. Each stimulus was cropped to fit a 289 (width) by 338 pixel (height) canvas. At a 57 cm viewing distance, the base faces comprised approximately 5° (distance between end points of eyebrows) by 6° (distance between eyebrow and bottom lip) of visual angle.

Using Adobe Photoshop the eight base faces were then subject to the following six (two-fold) changes composing the conditions implemented in the present study. Three conditions involved "featural" changes (of the eyes, nose and mouth) and three involved "relative distance" changes (inter-ocular, eyes–nose and nose–mouth distance). The extent and types of changes for both featural and second-order changes were similar to those employed in previous studies (Barton et al., 2001, 2002; Barton and Cherkasova, 2005; Goffaux and Rossion, 2007). The inter-ocular distance (eyes horizontal – EH) was either increased or decreased by moving each eye inward or outward by 10 pixels. The distance between the eyes and nose (eyes vertical – EV) was in- or decreased by elevating or lowering both eyes (along with the eyebrows) by 15 pixels. The distance between the nose and the mouth was increased or decreased by elevating or lowering the mouth by 12 pixels (mouth vertical – MV). The feature conditions consisted either of an increase or decrease of brightness for the eyes (eyes feature – Ef), or replacing the mouth (mouth feature – Mf) or nose (nose feature – Nf) with the respective features of two other base faces. Thus, there were six conditions (type of change) with two different instances per change type/base face (see Fig. 2b).

2.3. Procedure

In both Experiments 1 and 2 participants completed a two alternative forced-choice (2AFC) simultaneous matching task using the same stimuli. Each trial consisted of presentation of three equidistant face stimuli. Target stimuli were always located centrally above two probes, one of which was identical to the target; each target was, at random, a base or modified face. The stimuli were always presented in the same location; jittering stimulus location was considered negligible as the lack of texture and contour information was expected to lend sufficient task difficulty. Presentation time was unlimited; consecutive trials were initiated with a 1 sec interval after each response. Participants were instructed to indicate as accurately and rapidly as possible which of the two probes was identical to the target above by pressing a right or left key, respectively. Each possible pair of probes was presented twice involving a right and left response, respectively in order to avoid response bias.

In Experiment 1, participants were naïve concerning the manipulations according to which the stimuli differed randomly on a trial-by-trial basis. Before the actual experiment commenced, participants completed four practice trials, which were excluded from subsequent analyses. Given that there were eight base faces which were changed in a two-fold manner for each of the six conditions, the experiment consisted of the presentation of 192 trials (32 per condition, 16 for each direction of change), separated into four blocks of equal length with interleaved pauses. All control participants

Table 1 – Accuracy scores, raw and normalized RTs (SEs) per condition and subject (group) for Experiment 1.

Condition	Younger controls	AM1	AM2	PS
Accuracy				
EH	.92 (.016)	.98 (.016)	.98 (.016)	.64 (.060)
Ef	.89 (.043)	.97 (.022)	.95 (.027)	.63 (.061)
EV	.79 (.041)	.81 (.049)	.92 (.034)	.73 (.056)
Mf	.90 (.024)	.95 (.027)	.98 (.016)	.89 (.039)
MV	.84 (.026)	.88 (.042)	.91 (.037)	1.00 (.000)
NF	.83 (.038)	.83 (.048)	.92 (.034)	.83 (.048)
Raw RTs				
EH	2864 (312)	5720 (346)	4382 (294)	20626 (2272)
Ef	2442 (220)	3130 (266)	4459 (279)	25132 (2961)
EV	4368 (641)	10523 (654)	8245 (731)	23712 (3353)
Mf	2828 (74)	3823 (210)	2677 (148)	11495 (1231)
MV	3774 (432)	7472 (529)	7477 (543)	12243 (1570)
NF	3421 (232)	6533 (500)	5134 (560)	15900 (1708)
Normalized RTs				
EH	.87 (.04)	.94 (.06)	.82 (.05)	1.19 (.13)
Ef	1.29 (.09)	.52 (.11)	.83 (.06)	1.45 (.17)
EV	.78 (.07)	1.73 (.04)	1.54 (.14)	1.36 (.19)
Mf	.91 (.06)	.63 (.03)	.5 (.03)	.66 (.07)
MV	1.15 (.06)	1.23 (.09)	1.4 (.1)	.70 (.09)
NF	1.08 (.06)	1.08 (.08)	.96 (.1)	.91 (.10)

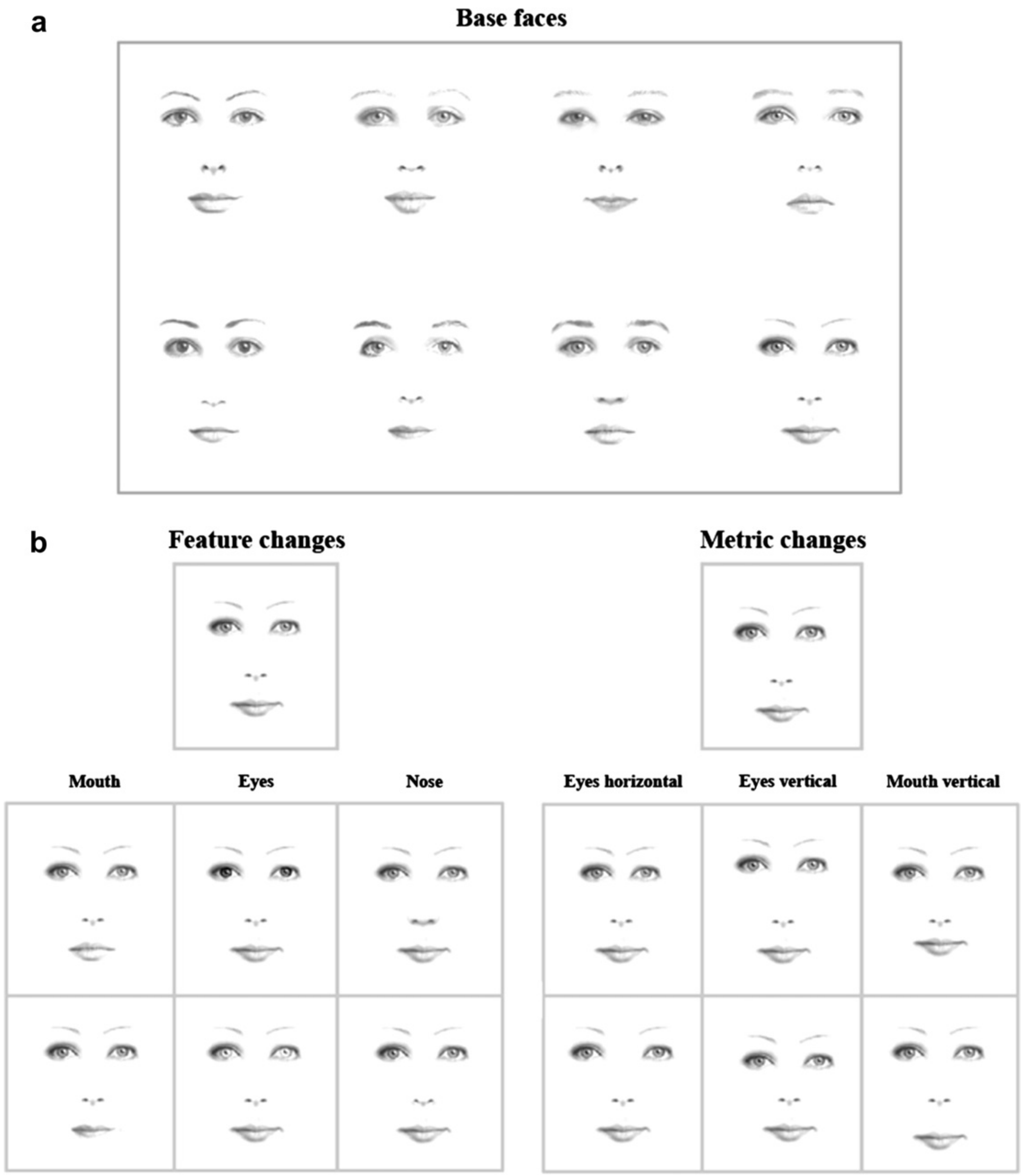

Fig. 2 – Stimuli used for Experiments 1 and 2. a. The eight base faces. b. Changes of features and relative distances. Feature changes included swapping the mouth or nose, as well as in- or decrease the brightness of the eyes, respectively. Changes of relative distances between features included in- and decrease of the inter-ocular distance (EH) as well as elevation and lowering of the eyes or mouth (EV/MV).

completed Experiment 1 twice (resulting in a total of 64 trials per condition independent of direction of change). Due to the fact that we expected PS to perform much slower than control participants, the experimental script used to acquire her data was divided into shorter subtests. The first one (containing 16 trials for each of the six conditions) was completed in spring 2006 (confirming our expectation her average responses were about 7 times as slow as those of age-matched controls). The remaining trials (48 per condition) were acquired in fall 2007 using 6 blocks amongst which the missing trials were randomly assigned. In total, all participants performed an equal amount of trials for each condition.

Experiment 2 differed from the first in that the types of manipulations according to which target and probes differed were presented in blocks (again with interleaved pauses). Additionally to this, the type of change to be discriminated was revealed prior to each block (e.g., ''In this block the color of the eyes will be diagnostic for detecting the target face''). The task was again a simultaneous 2AFC matching with each trial being terminated by participants' responses and a 2 sec ISI between consecutive trials. Prior to the actual experiment, participants practiced discrimination for each of the changes applied (3 practice trials per type of change, all excluded from subsequent analyses), upon which the actual experiment commenced. Participants completed two sessions of this experiment. For this matter two tests (differing with respect to order of experimental blocks, i.e., change types presented) were utilized; order of blocks was randomly assigned to all participants. In total for the younger and age-matched controls as well as PS we therefore obtained 96 trials per condition, which were subject to subsequent analyses. Note that PS completed 2 sessions, as did controls, as the instructions lead to a dramatic decrease in RTs (see Results).

Given the nature of the two experiments reported here, all participants inevitably had to complete Experiment 1 before Experiment 2. We acknowledge that this fixed order represents an unavoidable confound. However, as our aim is to investigate the performance of the patient PS under conditions of uncertainty and certainty, we would like to emphasize the importance of comparing the performance patterns *across* experiments. Given the complexity of a joint analysis of both experiments (due to the numerous factors), we will treat each one separately in terms of the statistical analyses.

For both experiments participants were seated in a quiet and dark room, 60 cm from the 17-inch PC monitor (60 Hz refresh rate; 1280×1024 pixel resolution). All stimuli were presented on a white background. The stimulus presentation was controlled using E-prime 1.1.

3. Results

3.1. *Experiment 1: uncertainty regarding the diagnostic facial cues*

Fig. 3a–c illustrate the mean accuracy rates for each experimental condition separately for the younger ($n = 10$) and two age-matched controls as well as PS; mean RTs per participant (group) are displayed together in Fig. 3d.

The data of the younger controls ranged between 79% and 92% across the 6 conditions (Fig. 3a). They were subject to a one-way repeated measures analysis of variance (ANOVA) which revealed a significant effect of condition ($F_{5,45} = 3.71$, $p = .007$). However, post-hoc *t*-tests (Tukey honestly significant difference – HSD) indicated that this effect was primarily due to lower accuracy rates in the condition EV (79%) as compared to EH (92%; $p < .01$; marginally significant for Ef *vs* EV: $p = .056$; Fig. 3). Thus, two conditions in which the diagnostic cue was located on the eyes rendered the best performance, but one (EV) was associated with the lowest performance. Considering all conditions involving the upper part of the face (eyes: EV, EH, Ef) as compared to the conditions involving the lower part of the face (mouth and nose: Mf, MV, Nf) in a post-hoc contrast, there were no significant differences ($p = .7$). Even though this comparison is not independent of the previous one, conditions involving distances between features (EV, EH, MV) were not processed better than conditions involving local modifications (Nf, Mf, Ef) overall ($p = .41$).

The results of the age-matched controls in accuracy were good (all above 82%), comparable to those of younger controls, except that the condition EV was performed slightly below the other conditions for one age-matched control, in line with observations made on the younger participants (Fig. 3b; Table 1).

To summarize, with respect to accuracy scores, both younger and age-matched controls were least efficient for the condition EV. There was no region-dependent difference in accuracy, along with no difference between discriminating relative distances as opposed to featural changes.

PS' accuracy rates ranged from 63% to 100% across the 6 conditions, which was significantly better than chance level overall (79%, $p < .0001$) but significantly less accurate than each of the controls (χ^2 for equality of two proportions, 92.5%; $ps < .0001$). Above this, she was generally much slower than all controls, taking more than 18 sec on average per trial (Fig. 3d; Table 1).

At an observational level, all conditions involving changes at the level of the eyes were associated with the lowest performance for PS (63–73%), while she appeared to perform much better for the conditions involving the mouth and the nose (83–100%, Fig. 3c). This was confirmed by a statistical analysis (ANOVA) on the items for PS, revealing significant differences between conditions ($F_{5,315} = 19.7$, $p < .001$). In contrast to the normal controls, every single condition with changes on the eyes was performed less well than each of the conditions involving modifications on the lower parts of the face (all $ps < .001$) with the exception of EV versus NF ($p = .3$). The condition MV was performed at ceiling (100%) and better than all other conditions, except for the condition involving a change of the mouth shape (MF; $p = .18$). Unsurprisingly, considering all conditions involving the upper part of the face (eyes: EV, EH, Ef) compared to the conditions involving the lower part of the face (mouth and nose: Mf, MV, Nf), a post-hoc contrast gave rise to a highly significant advantage for the lower part of the face ($p < .001$). Also, the conditions involving distances between features (EV, EH, MV) were not processed better than the conditions involving local modifications (Nf, Mf, Ef) overall ($p = .6$).

PS' performance was below 2SDs of each of the normal age-matched controls (to which she was compared at the single-subject level, individually) for 2 conditions only: EH (judging inter-ocular distance) and Ef (featural eye change), while her performance was at ceiling, and more than 2SDs above controls for detecting changes at the level of the mouth (Fig. 3b,c; Table 1).

Thus, contrary to controls, PS displayed a strong regional dissociation, with superior performance for changes occurring in the lower face region. Local featural changes were not associated with superior performance as compared to relative distance changes.

Regarding correct RTs, there were significant differences among conditions for normal control participants ($F_{5,45} = 7.83$, $p < .001$). Post-hoc *t*-tests indicated that this effect was primarily due to elevated RTs for EV as compared to EH ($p < .02$), Ef ($p < .02$) and Mf ($p < .01$), in line with accuracy scores. Considering all conditions involving the upper part of the face (eyes: EV, EH, Ef) as compared to the conditions involving the lower part of the face (mouth and nose: Mf, MV, Nf) in a post-hoc contrast, there were no significant differences ($p = .36$). However, conditions involving distances between features (EV, EH, MV) were processed slightly slower overall than conditions involving local modifications (Nf, Mf, Ef) (marginally significant, $p = .07$).

Thus, in line with the accuracy scores, no regional dissociation was found for younger controls; the same held for

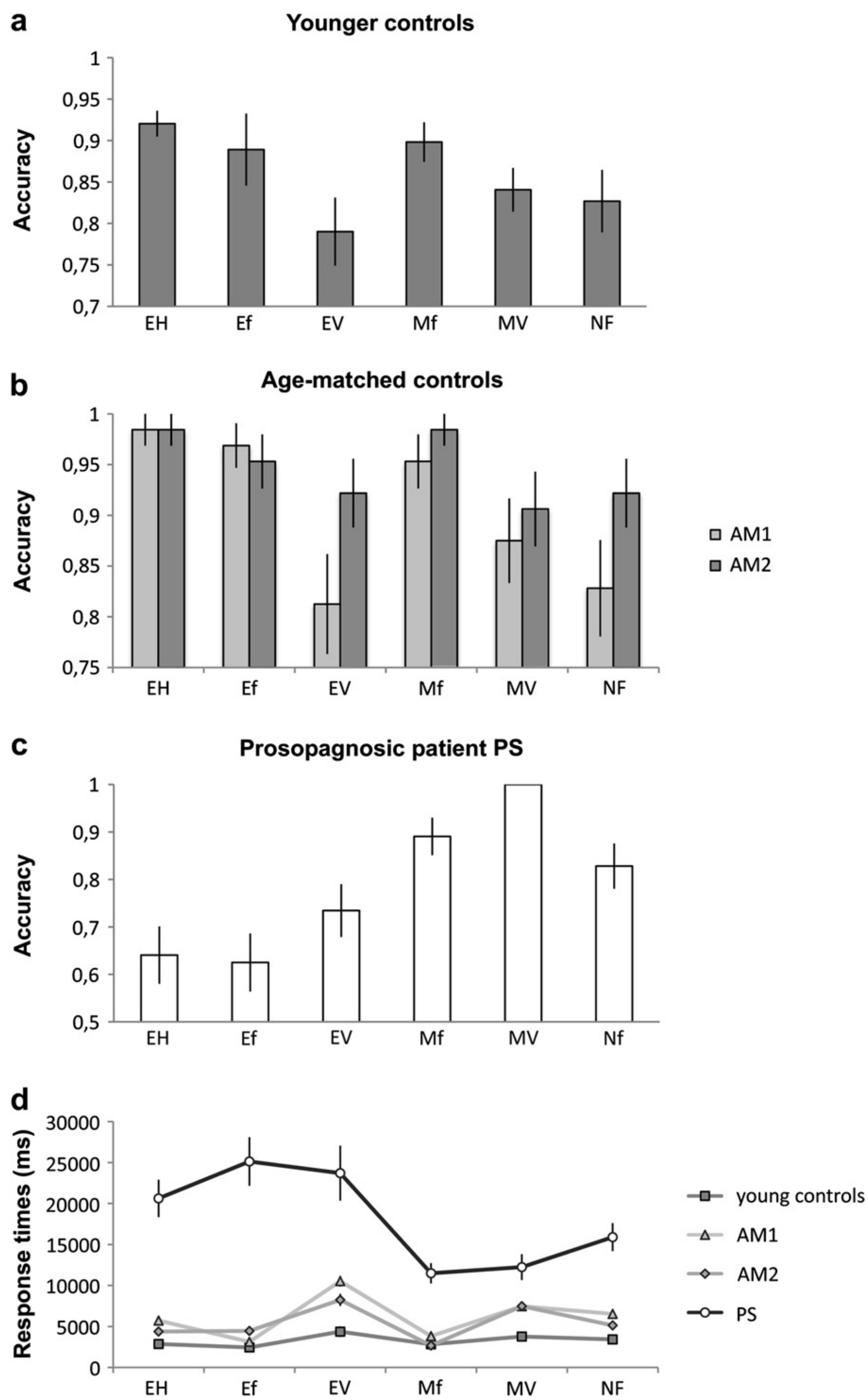

Fig. 3 – Performance profiles for Experiment 1. a–c. Accuracy scores (SEs) for younger and age-matched controls, as well as PS are presented separately for each experimental condition (EH; Ef; EV; Mf; MV; Nf). d. RTs for all participants across conditions.

relational distances as opposed to featural information, and EV remained the most difficult condition (see Fig. 3d, Table 1).

With respect to RTs, the age-matched controls were much slower (2.6–10.5 sec) than younger controls (2.8–4.4 sec) (Table 1). PS was still much slower than these normal controls in all of the conditions in the experiment (range of RTs for PS: 11.5 msec to 25 sec; see Fig. 3d, Table 1). However, in line with her accuracy rates, PS responded much "faster" for conditions involving the mouth (11–12 sec) or the nose (ca. 15 sec) than any change at the level of the eyes (above 20 sec) (Fig. 3d, Table 1). This was confirmed statistically, with a highly significant main effect of condition ($F_{5,190} = 51.8$, $p < .0001$). She was much faster for the conditions involving the lower part of the face (Mf, MV, Nf) than the conditions involving the eyes ($p < .0001$), which parallels the findings obtained with respect to her accuracy scores.

Across all conditions PS was slower than the younger as well as the age-matched controls (Fig. 3d). However, in order to compare PS' relative RTs to those of the controls in the different conditions, the RTs were normalized by dividing the value for each condition by the average RT across all conditions, separately for each participant (Table 1). This revealed that PS' RTs were relatively higher for the condition EH as compared to controls (>2SDs), while she was relatively faster for the MV condition (<2SDs), which is in line with her accuracy data.

In summary, this experiment confirmed that the patient PS is impaired and slowed down at processing individual faces (Rossion et al., 2003; Schiltz et al., 2006). However, when given unlimited time, her performance can be satisfactory, albeit remaining below normal performance for conditions involving a diagnostic cue at the level of the eyes, which is also in line with previously reported data reported with her in similar tasks (Caldara et al., 2005; Rossion et al., 2009) and in other patients (Bukach et al., 2008). PS also responded much slower in all the conditions involving the eyes as a diagnostic cue, both in absolute RTs compared to diagnostic cues located on other parts of the face, and relative to the controls. This pattern of results cannot be accounted for by differential levels of difficulty for normal observers, who, if anything, performed at least equally accurate and fast for the conditions involving changes at the level of the eyes compared to the lower part of the face (Fig. 3). Overall, in an individual face discrimination task with no instructions provided, the response profile for the prosopagnosic patient PS was in stark contrast with those obtained for normal controls.

3.2. *Experiment 2: removing uncertainty regarding the diagnostic cue*

Fig. 4a–c illustrate the mean accuracy rates for each experimental condition separately for the younger ($n = 10$), and two age-matched controls as well as PS; mean RTs per participant (group) are displayed in conjunction in Fig. 4d.

The data of the younger controls ranged between 93% and 97% across the 6 conditions (Fig. 4a). They were subject to a one-way repeated measures ANOVA, which revealed a significant effect of condition ($F_{5,45} = 4.72$, $p = .0015$). Post-hoc *t*-tests (Tukey HSD) indicated that this effect was again due to lower accuracy rates in the condition EV (93%) as compared to the other conditions, with exception of MV ($p = .12$; all other conditions: $ps < .024$). Considering all conditions involving the upper part of the face (eyes: EV, EH, Ef) as compared to the conditions involving the lower part of the face (mouth and nose: Mf, MV, Nf) in a post-hoc contrast, there were no significant differences ($p = .26$). Even though this comparison is not independent of the previous one, conditions involving local modifications (Nf, Mf, Ef) were processed slightly better than conditions involving distances between features (EV, EH, MV) overall (marginally significant, $p = .07$).

In summary, while—compared to the previous experiment—the normal younger controls improved their performance in this task, their response profiles for Experiment 1 (all trials randomized) and Experiment 2 (with conditions blocked) were remarkably similar (compare Figs. 3a and 4a). EV was unchangeably the most difficult condition; no regional differences were found, as was the case for contrasting performance for featural versus relational changes.

The results of the age-matched controls in accuracy were also close to ceiling (all above 97%), and comparable to those of younger controls (Fig. 4b; Table 2).

PS' accuracy rates improved dramatically, ranging from 72% to 100% across the 6 conditions, which was significantly better than chance level overall (88%, $p < .0001$) but significantly less accurate than age-matched controls (χ^2 for equality of two proportions, $ps < .0001$). She was still generally much slower than all controls, although her averaged RTs decreased substantially compared to Experiment 1 (compare Tables 1 and 2).

At an observational level, PS' response profile changed dramatically compared to Experiment 1: the condition associated with the highest accuracy rates was now the processing of an inter-relational change of the eyes (EH). She improved significantly for all conditions involving a modification at the level of the eyes, except for the condition with vertical modifications (EV) (Fig. 4c; Table 2). This was confirmed by an ANOVA on items, revealing significant differences between conditions ($F_{5,475} = 17.73$, $p < .001$). However, this was due to the condition EV being significantly lower than all other conditions ($ps < .001$), with the only other significant comparison revealing better performance being EH as compared to NF ($p = .018$).

PS' performance was below 2SDs of the normal controls for two conditions only: EV and Nf, while her performance was now in the normal range for the conditions EH and Ef.

Regarding correct RTs, there were significant differences between conditions for normal control participants ($F_{5,45} = 7.19$, $p < .001$), due to the lowest RTs for the EV condition (in line with accuracy scores) (Fig. 4d).

Again, the age-matched controls were much slower (1.4–4.4 sec) than younger controls (1.0–1.9 sec) (Table 2). PS was still much slower than these age-matched normal controls in all of the conditions (range of RTs for PS: 4.2–8.1 sec; Table 2). However, in this experiment PS was not faster for the conditions involving a modification at the level of the mouth as compared to the eyes (Table 2; Fig. 4d); Ef was the condition for which she was the fastest. This was confirmed statistically, with a highly significant main effect of condition ($F_{5,335} = 149.9$, $p < .0001$). She was much slower for EV trials as compared to all other conditions ($ps < .001$), but faster for Ef than all other conditions ($ps < .001$). The condition Nf was also associated with slower responses than all other conditions but EV ($ps < .01$).

As in Experiment 1, the RTs for each participant and condition were normalized by dividing the value for each condition by the average RT across all conditions, in order to compare PS' relative RTs to the age-matched controls in the different conditions (Table 2). This revealed that her RTs were relatively higher (>2SDs) for the condition Nf, while she was still *relatively* faster for the MV condition (<2SDs). However, and importantly, she was not relatively slowed down for any of the conditions involving the eyes (EV, EH, Ef).

Overall, these results again emphasize PS' difficulty with judging vertical eye changes, as only this condition was associated with both low accuracy and high RTs, as compared to EH and Ef. The region-dependent proficiency found in

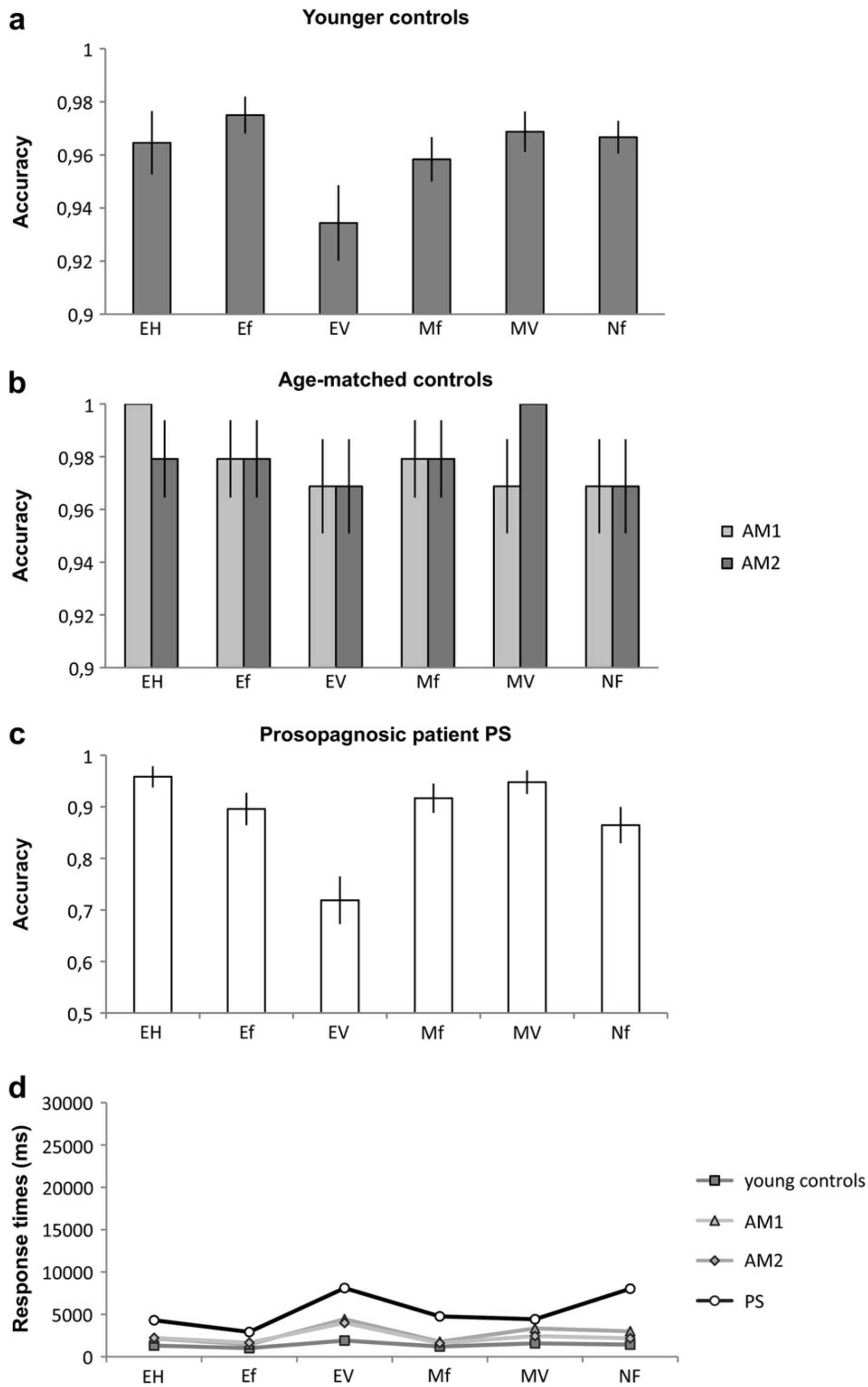

Fig. 4 – Performance profiles for Experiment 2. a–c. Accuracy scores (SEs) for younger and age-matched controls, as well as PS are presented separately for each experimental condition (EH; Ef; EV; Mf; MV; Nf). d. RTs for all participants across conditions.

Experiment 1 was no longer evident here; Nf and EV were associated with the lowest performance.

In summary removing uncertainty led to a general increase in performance in Experiment 2, most notably for PS, whose overall performance pattern became prominently identical to that of control participants—both in terms of accuracy (Figs. 3 and 4, a–c) and raw and normalized RTs (Figs. 5 and 6).

4. General discussion

The present investigation aimed at assessing the ability of PS, a case of AP with largely preserved low-level visual abilities and normal object recognition (Rossion et al., 2003; Schiltz et al., 2006; Sorger et al., 2007), to discriminate between faces

Table 2 – Accuracy scores, raw and normalized RTs (SEs) per condition and subject (group) for Experiment 2.

Condition	Younger controls	AM1	AM2	PS
Accuracy				
EH	.96 (.012)	1.00 (.000)	.98 (.015)	.96 (.021)
Ef	.98 (.007)	.98 (.015)	.98 (.015)	.90 (.031)
EV	.93 (.014)	.97 (.018)	.97 (.018)	.72 (.046)
Mf	.96 (.008)	.98 (.015)	.98 (.015)	.92 (.028)
MV	.97 (.008)	.97 (.018)	1.00 (.000)	.95 (.023)
NF	.97 (.006)	.97 (.018)	.97 (.018)	.86 (.035)
Raw RTs				
EH	1314 (108)	2151 (79)	2220 (90)	4306 (209)
Ef	1010 (73)	1450 (57)	1654 (64)	2920 (137)
EV	1908 (246)	4432 (179)	3998 (255)	8111 (466)
Mf	1202 (88)	1769 (69)	1595 (54)	4764 (278)
MV	1581 (159)	3339 (149)	2442 (98)	4424 (169)
NF	1432 (118)	3003 (200)	2171 (126)	8030 (622)
Normalized RTs				
EH	.94 (.02)	.8 (.03)	.95 (.04)	.81 (.04)
Ef	.73 (.03)	.54 (.02)	.7 (.03)	.55 (.03)
EV	1.33 (.06)	1.65 (.07)	1.7 (.11)	1.53 (.09)
Mf	.87 (.03)	.66 (.03)	.68 (.02)	.9 (.05)
MV	1.12 (.02)	1.25 (.06)	1.04 (.04)	.84 (.03)
NF	1.03 (.03)	1.12 (.07)	.92 (.05)	1.52 (.12)

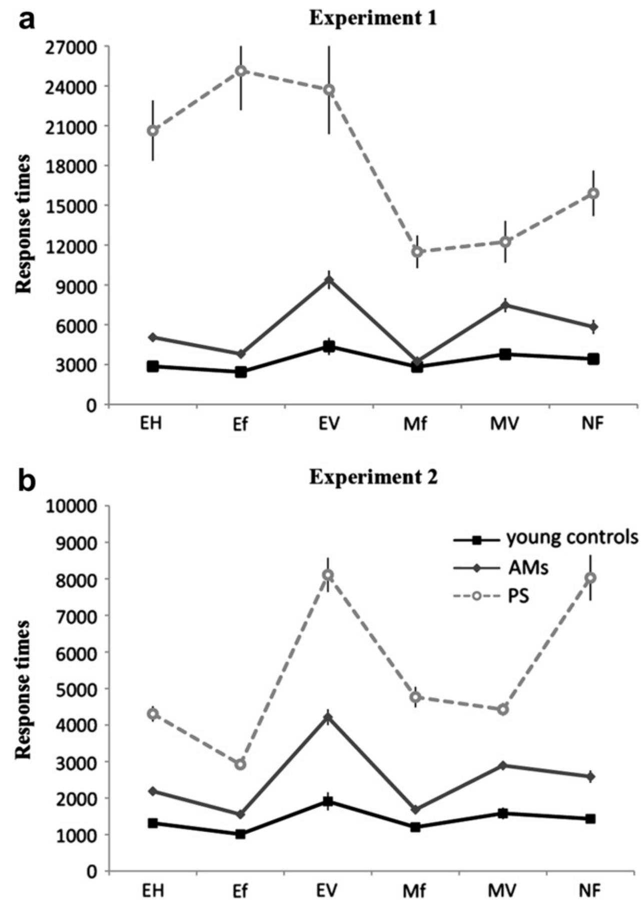

Fig. 5 – Response time profiles across both experiments for younger and age-matched controls, as well as PS for each experimental condition (EH; Ef; EV; Mf; MV; Nf). a. Correct RTs (SEs) for Experiment 1. b. Correct RTs (SEs) for Experiment 2.

differing either with respect to features or relative distances between these features.

The main outcome of this study is that, despite remaining slow and impaired relative to normal controls' performance, PS' response profile over 6 conditions involving diagnostic cues to discriminate faces became remarkably similar to that of the normal controls when she had prior knowledge about the nature and location of these cues diagnostic for discrimination.

Based on the present findings, we would like to argue that AP arises neither from an intrinsic inability to appreciate relative distances between features (e.g., Barton et al., 2002), nor a deficit in processing the area of the eyes per se (Caldara et al., 2005). Rather, we suggest that these patterns demonstrated by prosopagnosic patients, including PS, can be regarded as consequences of a single, common cause: the breakdown of a process that automatically resolves ambiguity about the nature and location of diagnostic information for face individualization. This process could be defined as the *capacity to simultaneously integrate the multiple facial elements distributed over the entire face into a unique representation* (i.e., holistic face processing; Rossion, 2008a; see also Sergent, 1984; Levine and Calvanio, 1989; Farah et al., 1998). In the following we address a number of points with respect to the current literature on AP to clarify the position advocated here.

4.1. *AP and abnormal processing of the eye region*

In Experiment 1, during which participants were naïve regarding the cue diagnostic for efficient discrimination, PS' performance was significantly inferior to that of controls for processing the inter-ocular distance, which is in concert with previous findings of impaired discrimination of inter-ocular changes (Barton et al., 2002; Bukach et al., 2006). Furthermore, she was also inefficient at discriminating featural changes of the eyes. Therefore, these results replicate her deficit of processing the eye region (Caldara et al., 2005; Ramon and Rossion, 2007; Rossion et al., 2009). This pattern has also been documented for several other cases of AP, with different lesion localizations (Bukach et al., 2006; see also Barton, 2008). In sum, there is evidence in the face processing literature that the reduced sensitivity to diagnostic information at the level of the eyes can be generalized over several cases of AP, even though the associated low-level impairments in many patients may modify this pattern (e.g., Barton et al., 2002).

4.2. *AP and processing of relative distances between features*

In the introduction we referred to one account of AP, which states a functional association between face-related deficits and the perception of inter-feature distances, respectively (Barton et al., 2002). In addition to her impairment at processing information within the eye region, our initial exploratory experiments demonstrated that PS could be extremely poor at detecting changes of relative distances between features that were instantaneously detected by normal observers. In a previous study, we also found that compared to normal

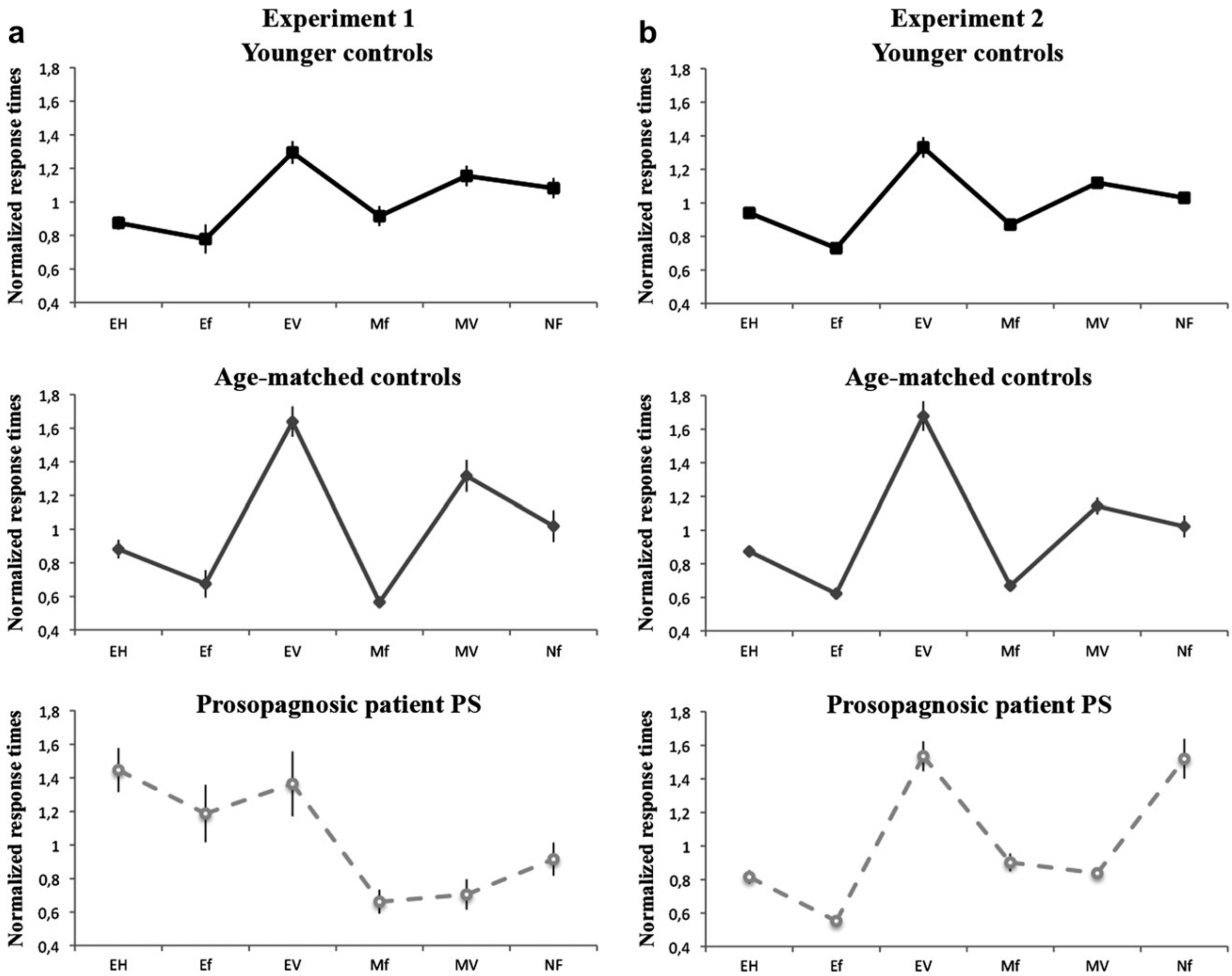

Fig. 6 – Normalized response time profiles for younger and age-matched controls, as well as PS are presented separately for each experimental condition (EH; Ef; EV; Mf; MV; Nf). a. Normalized RTs (SEs) for Experiment 1. b. Normalized RTs (SEs) for Experiment 2.

controls, PS was particularly slow for mouth-nose distance and inter-ocular distance judgments (Rossion et al., 2009, Fig. 2).

These observations suggest that, if *all possible* facial manipulations are included, and patients are naïve regarding the cue diagnostic for discrimination, two particularly large impairments become observable: deficient perception of relative distances in general (Barton et al., 2002; Joubert et al., 2003; Barton and Cherkasova, 2005; Barton, 2008), as well as abnormal processing of the eye region in particular (Caldara et al., 2005; Ramon and Rossion, 2007; Barton, 2008; Rossion et al., 2009). Importantly, this holds despite inter-individual differences in lesion sites and experimental settings between studies. This association suggests that key characteristics of prosopagnosia could be explained in terms of a common impaired process.

4.3. *The impact of prior information about diagnostic cues for facial discrimination*

In Experiment 2 all participants were informed as to which specific type/location of change was diagnostic for discrimination, and their performance improved. More importantly, PS improved specifically for all conditions involving the eyes. This indicates that her apparent advantage for processing the mouth (and presumably that of other prosopagnosic patients) is not absolute, but directly related to the fact that *at her own choice* she prefers to use the mouth as a cue for face discrimination. Supporting this claim, eye movement recordings of the patient PS during face identification indicate that she first and foremost fixates on the mouth (Orban de Xivry et al., 2008). Furthermore, PS' performance improved substantially for a condition involving relative distances (inter-ocular distance, EH), indicating that her deficit cannot be attributed to generally impaired processing of the latter.

Most interestingly, with prior knowledge PS displayed a performance pattern that, across all conditions, was strikingly similar to that of the controls (see Fig. 4). Thus, the relative deficiency for processing the eyes and relative distances appeared to depend on prior knowledge about the diagnosticity of a given cue in the task. This again suggests that key characteristics of prosopagnosia can be explained in terms of an impaired process, which allows normal observers to identify rapidly and efficiently the cue(s) diagnostic for face individualization.

4.4. *A holistic face processing account of acquired prosopagnosia*

To summarize, the present investigation demonstrates that it is difficult to attribute AP to an absolute processing deficit of judging relative distances between features, and/or the diagnosticity of the eye region per se. Rather, we believe that both of these effects reflect a common underlying cause: an impairment of holistic face processing. In line with earlier proposals (Sergent, 1984; Young et al., 1987; Tanaka and Farah, 1993), we conceptualize this ability as a mechanism that enables *simultaneous integration of multiple, distally located facial features into a unified, individual face representation* (Rossion, 2008a).

For normal observers, this process enables facial features to be processed in parallel, across a relatively wide range, as a *unique entity*. This ability makes face processing quite efficient, despite the fact that deriving a representation from a complex visual pattern for discrimination amongst other similar-looking patterns is an intricate task. The complexity and high processing demands of face processing become evident in cases of prosopagnosia: deficient holistic processing causes the patients to revert to serial processing of the individual features, over a small spatial window. As a consequence, certain types of information become less diagnostic. The region of the eyes in particular contains many individual elements, therefore its processing becomes time- and resource-consuming. In the same vein, perceiving relative distances between features is particularly difficult (with certain inter-feature distances being more difficult than others—depending on the spatial range they cover). In summary, an impairment of processing individual faces holistically may well account for both characteristics previously associated with prosopagnosia. Beyond the logical arguments developed here, several observations support this view.

First, as indicated above, a primary advantage of holistic processing is that it resolves ambiguity about the nature and location of diagnostic cues on the face. Since the face is processed as a single unit, a change in a given feature affects the perception of other features.

Thus, while resolving ambiguity for diagnostic cues in a difficult face matching task can generally improve normal observers' performance and speed, their *profile* of response was not affected much. However, for a prosopagnosic patient deprived of holistic processing, resolving ambiguity for diagnostic cues should lead to a more normal profile of performance across the different conditions—which is precisely what we observed for PS. There is evidence that this kind of finding could be generalized to other cases of AP. Barton et al. (2002) reported that some patients could substantially improve their performance for mouth position discrimination if informed about which region was modified or if trials for this condition were presented in succession (see also Joubert et al., 2003). Similarly, the patient LR's initial impairment for judging inter-ocular distances vanished when confronted with blocked trials of this condition (Bukach et al., 2006).

Second, the lack of holistic processing in AP is reflected by the fact that increased performance for one type of change (due to prior information or change of strategy) can have its costs. For instance, when focusing on the eyes, LR was unable to simultaneously extract information from the mouth (Bukach et al., 2006). In our preliminary investigation of the patient PS, we also found that her performance at discriminating faces based on the mouth trials decreased as her performance with the eyes increased (Fig. 1b–c). These observations suggest that the patients cannot process multiple diagnostic sources of information simultaneously. This is in sharp contrast to controls, who perform at the same level for the eyes, even when mouth changes are more frequent in the experiment (Barton et al., 2001; Malcolm et al., 2004).

Third, previous studies using different paradigms (e.g., the presence of context for feature/face recognition or the abnormal effect of inversion) have shown that AP is associated with holistic processing impairments (e.g., Levine and Calvanio, 1989; Sergent and Villemure, 1989; Sergent and Signoret, 1992; Farah et al., 1995; Saumier et al., 2001; Boutsen and Humphreys, 2002; Marotta et al., 2002; Delvenne et al., 2004).

This is also the case for the patient PS, for whom we have independent evidence of abnormal holistic face processing. While for normal observers face identification can be performed efficiently by fixating on a central point below the eyes (Hsiao and Cottrell, 2008; Orban de Xivry et al., 2008), PS' fixations during familiar face identification were always located either exactly on the mouth (60% of the time) or on either eye (Orban de Xivry et al., 2008), suggesting a feature-by-feature, local analysis. Beyond this, evidence using both the composite face and whole-part advantage paradigms (Tanaka and Farah, 1993; Young et al., 1987) indicates that PS' holistic processing of individual faces is strongly deficient (Ramon et al., submitted for publication).

Fourth, another aspect supporting the assumption that integration of multiple elements over a relatively wide range is a critical factor for intact face recognition, is the fact that PS displayed the least increase in performance for vertical eye displacements (EV). This is particularly interesting in the light of recent evidence from face inversion studies with normal observers that have demonstrated that the entire face needs to be taken into account in order to accurately appreciate EV changes (Goffaux and Rossion, 2007; Sekunova and Barton, 2007). That is, even when informed about the nature of this cue, judging the position of the eyes (along the vertical axis of the face) depends on their relative position to the nose and mouth, while judging the inter-ocular distance or the nose-mouth distance can be performed more locally (Sekunova and Barton, 2007). Hence, it is not so surprising that PS remained strikingly impaired in this condition (EV) in Experiment 2.

Based on these reports and our observations, we suggest that an impairment of holistic processing as a common underlying deficit can account for similar observations across cases of AP—in particular for the impairment at processing regions of the face containing multiple elements, as well as relative distances between features. This holds for patients presenting with varying lesion localization, etiologies and associated deficits.

Before concluding, we would like to mention three brief points, in order to minimize any confusion that may arise from this theoretical proposal.

First, we would like to emphasize that PS' dramatic improvement given prior information concerning the nature of the diagnostic cue does *not* indicate normal face processing, and would certainly be of no help in real-life circumstances. What happened in Experiment 2 was that her feature-based search-strategy became *relatively* more efficient: she simply no longer had to sample a number of available features, but only a single one. Nevertheless, she processed the facial information differently than normal participants, as reflected by her prolonged RTs (which is specific to faces; see e.g., Schiltz et al., 2006). This can be easily understood, since normal observers, even when being able to focus on a single facial cue, benefit from the facial context that modifies their perception of the whole face (Young et al., 1987; Tanaka and Farah, 1993; Tanaka and Sengco, 1997). Moreover, prior knowledge concerning the diagnostic cue for individuation cannot prove beneficial in standard tasks of face processing or real-life situations, as the facial stimuli encountered do not differ by means of only a single dimension (i.e., a feature, or relative distance between two or more features). In other words, knowing that for normal observers the eyes are the most diagnostic cue(s) for individuation cannot be regarded as a potential for prosopagnosics to overcome their difficulties—for normal observers the eyes' diagnosticity critically depends on their preserved ability to process faces holistically.

Second, the hypothesis of a lack of holistic processing in AP as defined here should not be confounded with a mere attentional account of this impairment. Like normal observers, the prosopagnosic patient tested here appears to be perfectly able to allocate attention to a given feature in the face display. However, in doing so, the features of the face that are out of the focus of attention do not influence her judgment, unlike what is found for normal observers (e.g., as in the well-known composite face effect; see Young et al., 1987). This reduction of the spatial window of analysis—or perceptual field—is not general, but applies only when the patient has to *individualize faces*. In other circumstances, for instance when judging local or global letters in hierarchical patterns (Navon test; Navon, 1977) or detecting a face based on the global organization of the constituent elements (e.g., a Mooney face), the patient PS appears to show normal behavior (Dricot et al., submitted for publication).

Finally, one may ask how prosopagnosic patients with different lesion localization might all show a common functional impairment—perhaps to a different extent—at processing individual faces holistically. One reason may be that damage to any node of the underlying distributed cortical face processing network (Sergent and Signoret, 1992; Haxby et al., 2000) impinges on the functional integrity of other areas in this network (Fox et al., 2008; Rossion, 2008b). In this way, a critical aspect of face processing 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 ('fusiform face area' – 'FFA'; Rossion et al., 2003). However, this area—which subtends holistic face processing in the normal brain (Schiltz and Rossion, 2006)—does not present release from adaptation to identity in PS' brain (Schiltz et al., 2006), presumably lacking inputs from the posteriorly damaged right inferior occipital cortex. This illustrates 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 et al., 2001). In this framework, it may be that only lesions to face-sensitive areas of the cortical face network that are involved in other aspects of face processing than face identity (e.g., amygdala, anterior superior temporal sulcus) would not lead to a disruption of holistic face processing.

5. Conclusion

Different theoretical accounts have been proposed for two characteristics associated with AP, namely deficient processing of diagnostic information in the eye region, as well as impaired perception of the relative distances between facial features. Here we show that these two impairments, which were presented by a single case of AP, result from an inability to disambiguate the nature and location of the diagnostic cues when individualizing faces. Based on these observations, we suggest that impaired holistic face processing underlies the prosopagnosic deficit of this patient and presumably that of many other cases.

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