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Impaired holistic processing of unfamiliar individual faces in acquired prosopagnosia

Meike Ramon*, Thomas Busigny, Bruno Rossion

Université Catholique de Louvain, Louvain-la-Neuve, Belgium

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ABSTRACT

Prosopagnosia is an impairment at individualizing faces that classically follows brain damage. Several studies have reported observations supporting an impairment of holistic/configural face processing in acquired prosopagnosia. However, this issue may require more compelling evidence as the cases reported were generally patients suffering from integrative visual agnosia, and the sensitivity of the paradigms used to measure holistic/configural face processing in normal individuals remains unclear. Here we tested a well-characterized case of acquired prosopagnosia (PS) with no object recognition impairment, in five behavioral experiments (whole/part and composite face paradigms with unfamiliar faces). In all experiments, for normal observers we found that processing of a given facial feature was affected by the location and identity of the other features in a whole face configuration. In contrast, the patient's results over these experiments indicate that she encodes local facial information independently of the other features embedded in the whole facial context. These observations and a survey of the literature indicate that abnormal holistic processing of the individual face may be a characteristic hallmark of prosopagnosia following brain damage, perhaps with various degrees of severity.

1. Introduction

Brain damage to bilateral or right unilateral occipito-temporal regions can cause a massive impairment at recognizing familiar faces. This rare neurological condition has been termed 'prosopagnosia' (Bodamer, 1947) and has attained a considerable degree of popularity in the neuropsychological literature since the first clinical observations (Quaglino, Borelli, Della Sala & Young, 2003; Wigan, 1844). The clinical and anatomical conditions of prosopagnosia have been of great interest to cognitive neuroscientists willing to clarify the neuro-functional mechanisms of normal face processing. For instance, the study of prosopagnosia is at the origin of the idea that there are neural processes devoted exclusively to faces in the adult human brain (Bodamer, 1947). Anatomical descriptions of prosopagnosia have also provided the first and strongest evidence for the critical role of the right occipito-temporal cortex in face recognition (Meadows, 1974; Landis, Regard, Bliestle, & Kleihues, 1988; Michel, Poncet, & Signoret, 1989; Sergent & Signoret, 1992a; Barton, Press, Keenan, & O'Connor, 2002; Bouvier & Engel, 2006). However, despite the relatively large number of cases of acquired prosopagnosia (AP) reported since the first descriptions, there is yet no unified account for these patients' inability to recognize or discriminate individuals by means of their faces.

Following early proposals (e.g., Levine & Calvanio, 1989; Sergent & Villemure, 1989), it has been suggested that AP patients suffer from an inability to process faces configurally/holistically.[1] Levine and Calvanio (1989) described the patient LH as being unable to "*get an immediate overview of a face [. . .] as a whole at a single glance*" (p.159). Following experiments with non-face patterns and tests of visual closure, these authors concluded that AP represents a general loss of visual "*configural [i.e. holistic] processing*"—a view supported by subsequent observations.

A number of studies have inferred a deficit of holistic face processing (HP) in prosopagnosia from an abnormal effect of face inversion: contrary to controls the patients either showed a reduced effect, or no performance decrease at all (e.g., Gauthier,

* Corresponding author at: Université Catholique de Louvain (UCL), Faculté de Psychologie et des Sciences de l'Education (PSP), Unité de Cognition et Développement (CODE), Place Cardinal Mercier, 10, B-1348 Louvain-la-Neuve, Belgium.
Tel.: +32 10 47 30 27; fax: +32 10 47 37 74.
E-mail address: meike.ramon@uclouvain.be (M. Ramon).

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[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). Its empirical manifestation is characterized by the inter-dependence between facial features.

Behrmann, & Tarr, 1999; Marotta, McKeeff, & Behrmann, 2002; Delvenne, Seron, Coyette, & Rossion, 2004), or even a paradoxical superior performance with inverted faces (e.g., Farah, Wilson, Drain, & Tanaka, 1995; but see Busigny & Rossion, 2009). However, since the nature of the face inversion effect remains a matter of debate (Rossion, 2008a), abnormal effects of inversion in AP provide only indirect evidence that the cause of the processing impairment is a deficit of HP (see Busigny & Rossion, 2009, for a recent discussion).

Other authors have followed Levine and Calvanio's (1989) approach and showed general holistic processing impairments in AP with non-face stimuli (overlapping figures, Gestalt-completion figures, global texture, dot patterns, hierarchical Navon stimuli, . . . e.g., Evans, Heggs, Antoun, & Hodges, 1995; Takahashi, Kawamura, Hirayama, Shiota, & Isono, 1995; for a review of global/holistic processing in object perception in general see also Kimchi, 1992).

A lack of HP in prosopagnosia has been more directly and specifically inferred from observations made based on matching or priming experiments with schematic faces made of multiple features, and multidimensional analysis (Sergent & Villemure, 1989; Sergent & Signoret, 1992b; Saumier, Arguin, & Lassonde, 2001), or from whole–part interference paradigms such as the Thatcher illusion (Boutsen & Humphreys, 2002; Riddoch, Johnston, Bracewell, Boutsen, & Humphreys, 2008). Finally, some authors have emphasized the difficulty of AP patients in processing relative distances between features (Barton et al., 2002; Joubert et al., 2003), a type of information diagnostic for face individuation that has been characterized as "configural" (Carey, 1992; Maurer, Le Grand, & Mondloch, 2002).

Together, these studies have provided some evidence supporting the view that AP is characterized by a particular lack of the ability to integrate facial features into a global (i.e., holistic) representation. However, more compelling evidence to support the above-mentioned hypothesis may be necessary, for at least two reasons. First, all studies (with the exception of one case in Sergent & Signoret, 1992a, and one recent case by Riddoch et al., 2008) have tested patients presenting clear basic-level object recognition impairments (Levine & Calvanio, 1989; Sergent & Signoret, 1992a, two cases; Farah et al., 1995; Evans et al., 1995; Takahashi et al., 1995; de Gelder, Bachoud-Lévi, & Degos, 1998; Gauthier et al., 1999; Saumier et al., 2001; Barton et al., 2002; Boutsen & Humphreys, 2002; Marotta et al., 2002; Delvenne et al., 2004; Anaki, Kaufman, Freedman, & Moscovitch, 2007). Thus, while Levine and Calvanio's (1989) view is that AP represents a *general* loss of visual "*configural [i.e. holistic] processing*", this hypothesis may require further investigation from single case studies of patients presenting a *selective* deficit for face recognition, tested for their holistic processing abilities with face (rather then object) stimuli.

Second, there are two paradigms that have been used extensively in the behavioral literature with normal viewers to demonstrate HP: the composite face paradigm (Young, Hellawell, & Hay, 1987) and the whole-part paradigm (Tanaka & Farah, 1993). Both reveal effects that are acknowledged to demonstrate holistic processing of facial features (Maurer et al., 2002; McKone & Robbins, 2007; Rossion, 2008a). While variants of the whole/part paradigm have been tested with visual agnosic patients (e.g., Boutsen & Humphreys, 2002), the composite face paradigm, which is more consistently used and gives more robust holistic effects has not been tested in AP (see Le Grand, Mondloch, Maurer, & Brent, 2003, for composite face effects tested in congenital prosopagnosia). Since these effects have been well demonstrated in the normal population, and are acknowledged to be highly sensitive at measuring HP, an absence or reduction of composite and whole/part effects in a case of AP would provide strong evidence for HP difficulties.

Taking into account these issues, we tested HP of the prosopagnosic patient PS, who suffers from a selective deficit at recognizing and matching individual faces following brain damage (Rossion et al., 2003), applying both the whole/part and composite face paradigms, across five experiments. In line with previous proposals (e.g., Galton, 1883; Goldstein & Chance, 1980; Farah, Wilson, Drain, & Tanaka, 1998; Ingvalson & Wenger, 2005), here we conceptualize HP as the "*simultaneous perception of the multiple features of an individual face, that are integrated into a single global representation*" (Rossion, 2008a). A direct consequence of this holistic mode of processing is that normally a given facial feature cannot be processed independently of the other features. We hypothesize that the patient PS – deprived of this holistic mode of processing faces – would process a given facial feature without being influenced by other features of the whole face.

2. Case description

The patient PS has been described in detail elsewhere, both functionally and neuro-anatomically (Rossion et al., 2003; Caldara et al., 2005; Schiltz et al., 2006; Sorger, Goebel, Schiltz, & Rossion, 2007; Orban de Xivry, Ramon, Lefèvre, & Rossion, 2008). She sustained closed head injury in 1992, which caused extensive lesions, mainly to the right inferior occipital and the left mid-ventral cortex (mainly fusiform gyrus) (for all anatomical details see Sorger et al., 2007). She complains only of a profound difficulty in recognizing faces. PS can discriminate faces from other objects, but is impaired and particularly slow at recognizing faces at the individual level (Schiltz et al., 2006). She performs below normal range on the Benton Face Recognition Test (Benton & Van Allen, 1972) (Busigny & Rossion, 2009), and her low score on the Warrington Recognition Memory Test (Warrington, 1984) for faces characterizes her as impaired (see Table 1, Sorger et al., 2007). PS is not impaired at recognizing/discriminating objects, even at the subordinate level (Rossion et al., 2003; Schiltz et al., 2006). Her visual field is almost full (with exception of a small left paracentral scotoma), her visual acuity good (.8 for both eyes as tested in August 2003) and her color perception is in the normal lower range (Sorger et al., 2007).

3. Experimental studies of holistic processing

3.1. General methodological considerations

It is generally acknowledged that – apart from their difficulties at recognizing familiar faces (e.g., Benton, 1980) – AP patients present with impairments at matching unfamiliar faces at the individual level, either in terms of accuracy scores, or prolonged RTs due to the use of slow, piecemeal strategies (Farah, 1990; Davidoff & Landis, 1990; Delvenne et al., 2004). The patient PS is similar to other cases of AP in this respect: she is markedly impaired at recognizing familiar faces (personally familiar, or famous) and is also strongly deficient and particularly slow at discriminating individual unfamiliar faces, as well as matching different pictures of the same individuals (Rossion et al., 2003; Schiltz et al., 2006; Rossion, Kaiser, Bub, & Tanaka, 2009). Here, across a range of (unfamiliar face) matching tasks, we investigated the interactivity of processing facial parts. In all experiments the stimuli were presented until a response was provided in order to avoid putting the patient under pressure and chance level performance.

In the 2 experiments (1 and 2) involving the whole–part advantage paradigm, a target was presented, followed by two probe stimuli (simultaneously), and participants had to choose which one corresponded to the target. This forced-choice procedure could not be applied for the composite face experiments (3–5), which require "same" and "different" trials to be treated separately, given that the composite effect is observed only on "same" trials (Le Grand,

Mondloch, Maurer, & Brent, 2004; Michel, Rossion, Han, Chung, & Caldara, 2006; McKone & Robbins, 2007).

Since an absence of effect could also be found in any normal individual participant in a single experiment, we tested PS with many trials, over several experiments, in order to accumulate evidence for her impairment in HP. For each experiment, the paradigms were validated with a group of younger control participants (C1–C10), to which we added two age-matched controls (AMs) (3 in experiment 2; AM1–AM3).

In terms of analyses, outlier trials (above or below 3 standard deviations from the mean) were first rejected, subsequent to which we first investigated whether the predicted effects were presented by the group of normal controls, for both accuracy scores and correct RTs. In order to normalize for overall differences in these measures, we further computed individual integration indexes, reflecting the relative difference in performance across conditions. We compared PS' integration indexes to those of the normal controls using Crawford and Howell's (1998) modified *t*-test (one-tailed) for single-case studies. Additionally, we investigated whether the effects observed on the group level could be found in each control by means of χ^2-test of two proportions (unilateral) for accuracy scores, and independent samples *t*-tests for correct RTs between conditions.

3.2. Experiment 1: whole–part advantage

3.2.1. Rationale and hypothesis

In the whole–part advantage paradigm, discrimination of a given facial feature is superior in the presence (and correct organization) of the whole face compared, to the presentation of the feature in isolation. This effect is assumed to reflect the face processing system's natural integration of the features into

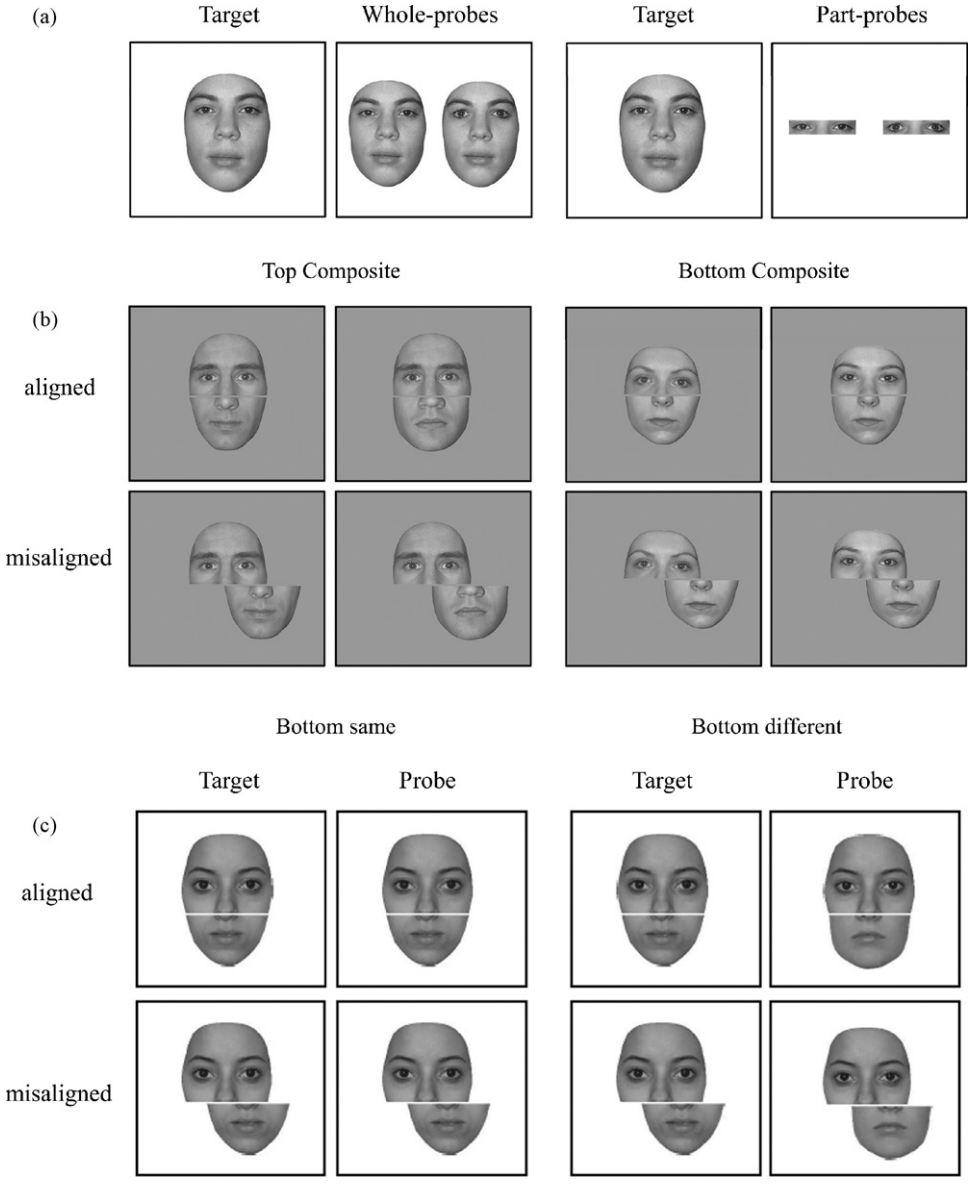

Fig. 1. Stimuli used in experiments 1–5. (a) Examples of stimuli used in experiments 1 and 2. Note: For both experiments identical stimuli were used; besides minor methodological differences experiment 2 can be regarded as an extension of experiment 1 in that the initially presented targets could also display face parts. (b) Examples of stimuli used in (i) experiment 3 (top composite) and (ii) experiment 4 (bottom composite). Note that instances of relevant "same" trials are displayed only, with the stimuli differing with respect to their bottom or top parts, respectively. (c) Examples of stimuli used in experiment 5. The left columns provide exemplar target stimuli (aligned or misaligned). The right columns present possible probes, which could be entirely identical to targets (same top, i.e. "same" response, and same bottom), differ with respect to bottoms (same top, i.e. "same" response, and different bottom), or completely different (different top, i.e. "different" response, and different bottom); only examples of relevant "same" trials are displayed.

a coherent whole percept. It is generally stronger for the eyes than other facial features (e.g., Tanaka & Farah, 1993; Pellicano & Rhodes, 2003), and is sometimes tested only for this part of the face (e.g., Michel et al., 2006).

3.2.2. Methods

3.2.2.1. Participants. Besides PS, 10 undergraduate students (age range—: 19–21; all from the Department of Psychology), and 2 AMs (56, 54 years) were tested. PS participated in this experiment when she was 53 years old.

3.2.2.2. Stimuli. Thirty grayscale full-front faces (neutral expression; half male), cropped of external features and free of facial hair or glasses, served as stimuli (ca. 200 × 250 pixels). For twenty faces, the original eyes were swapped with those of a different face; the remaining 10 faces served to create five nose and mouth-foils by swapping these features. Part stimuli were then created by isolating the relevant feature from these whole foil faces (20 isolated eyes, 5 noses, 5 mouths). Nose and mouth face stimuli were used for catch trials (1/3 of the trials; not analyzed) to avoid participants exclusively focusing on the eyes (see e.g., Goffaux & Rossion, 2006). Fig. 1a illustrates an example of a whole and part trial.

3.2.2.3. Procedure. Trials began with a centrally presented target (1500 ms). After a 300 ms ISI, two juxtaposed probe stimuli were presented until subjects responded which probe matched the target stimulus (by pressing a right or left key); trials were separated by an inter-trial interval (ITI) of 800 ms. Target stimuli were always whole faces, presented slightly larger than the probes. In the *whole display* condition, probes were whole faces, with one differing from the target by a single feature. In the *part display* condition, only the features were presented (see Fig. 1a). Each target and probe stimulus appeared twice; the location of probe presentation was counterbalanced. Participants completed 120 randomly presented trials (40 catch, 80 valid trials—40 per condition) preceded by 6 practice trials.

Participants were seated 60 cm from the 17-in. PC monitor (60 Hz refresh rate; 1280 × 1024 pixel resolution). Target stimuli subtended 9° × 6° of visual angle (VA); the size of probes varied depending on type (same size for whole probes; eyes, nose and mouth features were 1° × 5.5°, 2.5° × 2.5°, and 1.5° × 2.5° of VA).

3.2.3. Results

PS was better than chance level overall, scoring 66%, $p = .002$, but her performance was much lower than that of controls, who achieved 87% on average ($p = .001$) (Fig. 2a). She was also much slower overall, taking more than 4 s on average per trial.

In normal controls, a whole–part advantage was observed both for accuracy, $t(11) = 6.60$, $p < .0001$, and correct RTs, $t(11) = 2.53$, $p = .014$.

In order to investigate the relative advantage for whole as compared to part probes, we computed whole–part integration indexes for both behavioral measures {(whole − part)/(whole + part)}. Comparison of PS' whole–part integration indexes to those of the normal controls indicated that her whole–part effect in terms of accuracy was significantly lower than that of controls, $t(11) = 2.46$, $p = .016$; (RT: $t(11) = .92$, *ns*) (Fig. 2b).

Every single participant showed the whole–part superiority in terms of either accuracy or RTs, or both, except for C2 (who showed no effect in terms of accuracy, and a significant effect in the opposite direction for correct RTs, $p = .03$) (see Fig. 2c). While two controls' accuracy scores did not show significant whole–part effects in accuracy (AM1, $p = .09$; C10, $p = .054$), only three controls' did not show the effect in RTs (C6, $p = .053$; C7, $p = .27$; C8, $p = .15$; note however, that these 3 controls showed a large whole–part advantage in terms of accuracy). Thus, the general finding (with exception of C2) was superior performance for wholes as compared to parts, i.e. a whole–part advantage. Contrariwise, this whole–part advantage was not found for PS, who showed no effect, neither for accuracy, nor RTs ($p = .28$ and .31) (Fig. 2b and c).

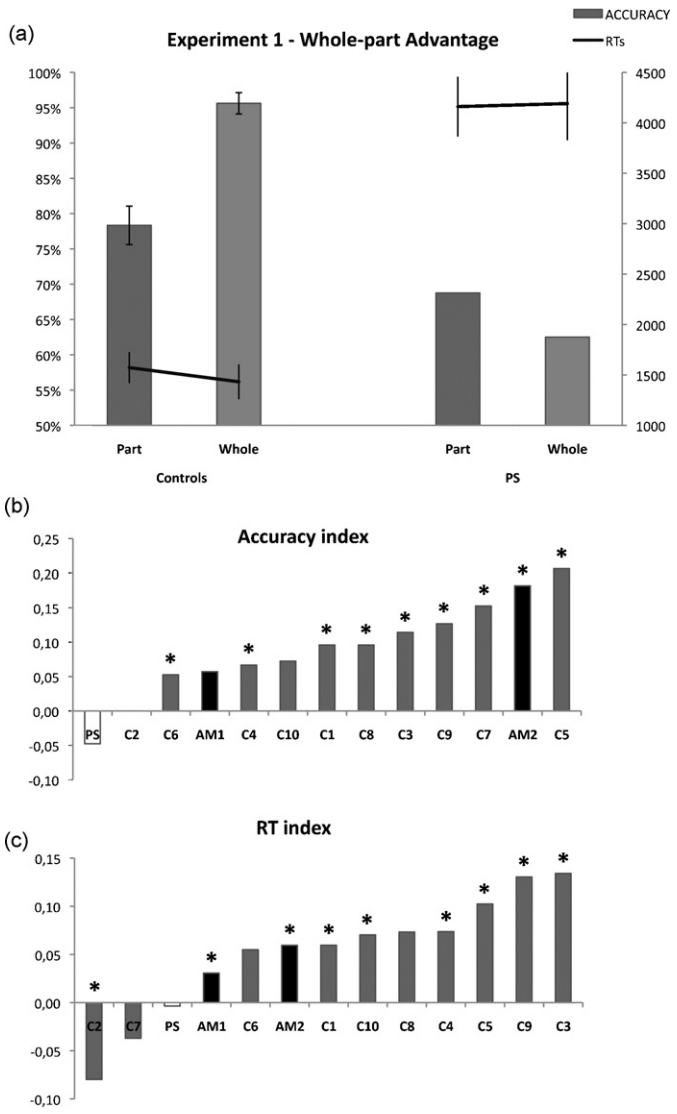

Fig. 2. Experiment 1: whole–part advantage. (a) Performance for normal controls and PS are displayed in the same graph for both accuracy and correct RTs (SE). (b) Accuracy and (c) RT indexes for each participant (ranked) represent normalized scores indicating the relative differences between the conditions in which probe stimuli were presented as "parts" or "whole faces", respectively. Asterisks indicate significant differences between both conditions on the single-subject level.

3.2.4. Discussion

PS was less efficient than controls in this task but she performed above chance level overall. Unlike controls, she did not show any advantage at processing the eyes as a feature embedded in context, as compared to its processing in isolation. Hence, her behavior can be interpreted as reflecting a lack of (positive) influence of the remaining facial features when processing the eyes. Rather than reflecting a kind of interference (of the whole to the parts, e.g., Farah et al., 1995; Boutsen & Humphreys, 2002), a more parsimonious interpretation of this observation could be that the prosopagnosic patient – deprived of HP – does not automatically detect which feature is diagnostic when a *whole* face is presented at recognition. However, when isolated eyes are presented, there

is no ambiguity regarding the nature of the feature to process, so the patient performs relatively more efficiently.

3.3. Experiment 2: whole–part–whole

The second experiment was carried out to strengthen and extend the observations made in experiment 1. Here, a full design was used in which the first stimulus could either be a whole or a part of a face. In line with other authors (Leder & Carbon, 2005), we reasoned that HP can be demonstrated in two different ways. First, the classical whole–part advantage (Tanaka & Farah, 1993), i.e. a benefit for recognizing features due to the presence of contextual information, should be observed when comparing "whole-to-whole" and "whole-to-part" trials. Beyond this we predicted superior performance in normal participants. when the format at encoding (i.e. target) and recognition (i.e. probes) are identical: "part-to-part" and "whole-to-whole" trials should be associated with superior performance as compared to those involving format changes (see Leder & Carbon, 2005).

3.3.1. Methods

3.3.1.1. Participants. We tested 10 undergraduate psychology students (age range: 19–21) and 3 AMs (56, 50, 57 years), none of which had participated in experiment 1. PS completed this experiment twice with an interleaved 8-month interval, in 2003 and 2004 (53, 54 years old).

3.3.1.2. Stimuli and procedure. The same stimuli as in experiment 1 were used (see Fig. 1a). The task and procedure was identical to experiment 1 unless specified (target presentation: 2000 ms; 500 ms ISI; 1000 ms ITI). Here however, targets were either full faces (*whole*-to-wholes and *whole*-to-parts trials), or isolated features (*part*-to-parts and *part*-to-wholes trials). The probe stimuli were identical to those used in experiment 1. Subjects completed a total of 240 trials (80 catch trials; 40 trials per condition analyzed; each target/probe stimulus appeared 4 times), which were separated in 4 blocks of equal length.

3.3.2. Results

PS was better than chance level overall, scoring 71%, $p < .0001$, but her performance below that of controls (who achieved 89% on average, $p < .0001$). She was also generally slower, taking 2.5–4 s on average per trial (controls' range: .8–1.8 s) (Fig. 3a).

The ANOVA on accuracy scores for all controls yielded significant main effects of both encoding format, $F(1,12) = 43.69$, $p < .0001$, and recognition format, $F(1,12) = 4.77$, $p < .05$. Most importantly, there was a significant interaction between the two factors, $F(1,12) = 24.24$, $p < .001$. Paired samples t-tests showed a whole–part advantage (whole–wholes *vs.* whole–parts, $t(12) = 4.77$, $p < .001$). There was also an advantage for the part–parts condition, as it was associated with higher accuracy than the part–wholes ($t(12) = 2.65$, $p = .01$).

For correct RTs, the ANOVA revealed a main effect of encoding format, $F(1,12) = 15.88$, $p < .01$, as well as recognition format, $F(1,12) = 6.68$, $p = .02$. Again, there was a highly significant interaction between the two factors, $F(1,12) = 38.15$, $p < .0001$. Paired samples t-tests showed a significant whole–part advantage for RTs, $t(12) = 2.37$, $p = .02$. The part–parts condition was also associated with smaller RTs than the part–wholes, $t(12) = 7.36$, $p < .0001$.

Integration indexes were computed individually for both accuracy scores and correct RTs. For each measure two different indexes (reflecting the relative advantage for format congruency between target and probes) were computed: one whole target and another for part target trials (see Fig. 3b and c).

Comparing PS' accuracy indexes to those of controls yielded a significant difference for whole-first indexes, $t(12) = 2.30$, $p = .02$, but not part first indexes, $p = .17$. Comparisons of RT indexes yielded no significant difference between PS and controls, neither for whole first ($p = .19$), nor part first indexes ($p = .11$), even though the trends were in the right directions (PS' performance was inferior to that of all controls).

At the individual level, 6 participants showed an advantage for whole–wholes over whole–parts in terms of accuracy, with only one showing a part–parts over part–wholes significant advantage (C6, $p \leq .05$). For correct RTs, 5 controls showed a significant whole–wholes over whole–parts advantage ($p < .05$), and all but one (AM2, $p = .07$) showed an advantage for part–parts over part–wholes ($p < .05$). Control C7 was the only one with a slightly divergent pattern (no difference between conditions for accuracy, longer RTs for whole–wholes as compared to whole–parts). Yet, this control showed a significant effect for part–parts vs. part–wholes. As for PS, she showed the lowest index in two variables (accuracy in whole first; RTs in part first) and had no significant effect in the right direction in any of the variables measures. In short, she was the only participant who showed an absence of any (positive or negative) influence of the whole face on the processing of facial parts (Fig. 3b and c).

3.3.3. Discussion

The results of experiment 2 replicate the previous observations and extend them to a condition in which the first stimulus is presented as a face part. While normal controls showed a clear advantage at discriminating two faces based on the eyes given format congruency at encoding and recognition, PS neither showed an advantage (whole–wholes *vs.* whole–parts) or disadvantage (part–parts vs. part–wholes) created by the context of the irrelevant facial features, which supports the hypothesis of abnormal HP for the patient PS.

However, there may be some limitations to the paradigm. First, while overall the whole–part paradigm leads to robust and replicable effects, the effects are not always very large and are not consistently found at the individual level (Figs. 2 and 3). Second, in the whole/part paradigm, there is no explicit instruction about which part of the face has to be encoded so that different observers may use different strategies when a whole face is presented at encoding. Third, we tested only the influence of the presence/absence of contextual facial information with respect to recognition of the eyes (nose/mouth trials served as catch trials, excluded from analyses), as the effects are most robust when performance is tested for this area in normal observers (e.g., Pellicano & Rhodes, 2003; Tanaka & Farah, 1993). However, the patient PS processes this area of the face particularly less efficiently than do normal observers (Caldara et al., 2005; Rossion et al., 2009).

For these reasons, we consider that converging evidence by means of another sensitive measure of holistic processing would be necessary to make stronger conclusions regarding the lack of HP in the prosopagnosic patient PS. The following experiments address these issues by further documenting PS' lack of reliance on holistic representations, for both the upper and lower parts of the face, using the composite face paradigm.

3.4. Experiment 3: top composite

3.4.1. Methods

3.4.1.1. Participants. PS, 10 new younger controls (mean age: 24.4 ± 4, four male; one left-handed), and 2 new AMs (50, 57) participated in this experiment. They all completed four consecutive sessions of the same experiment. The first two completed by PS were acquired consecutively as well, with a 6- and 10-month delay between the third and fourth session, respectively.

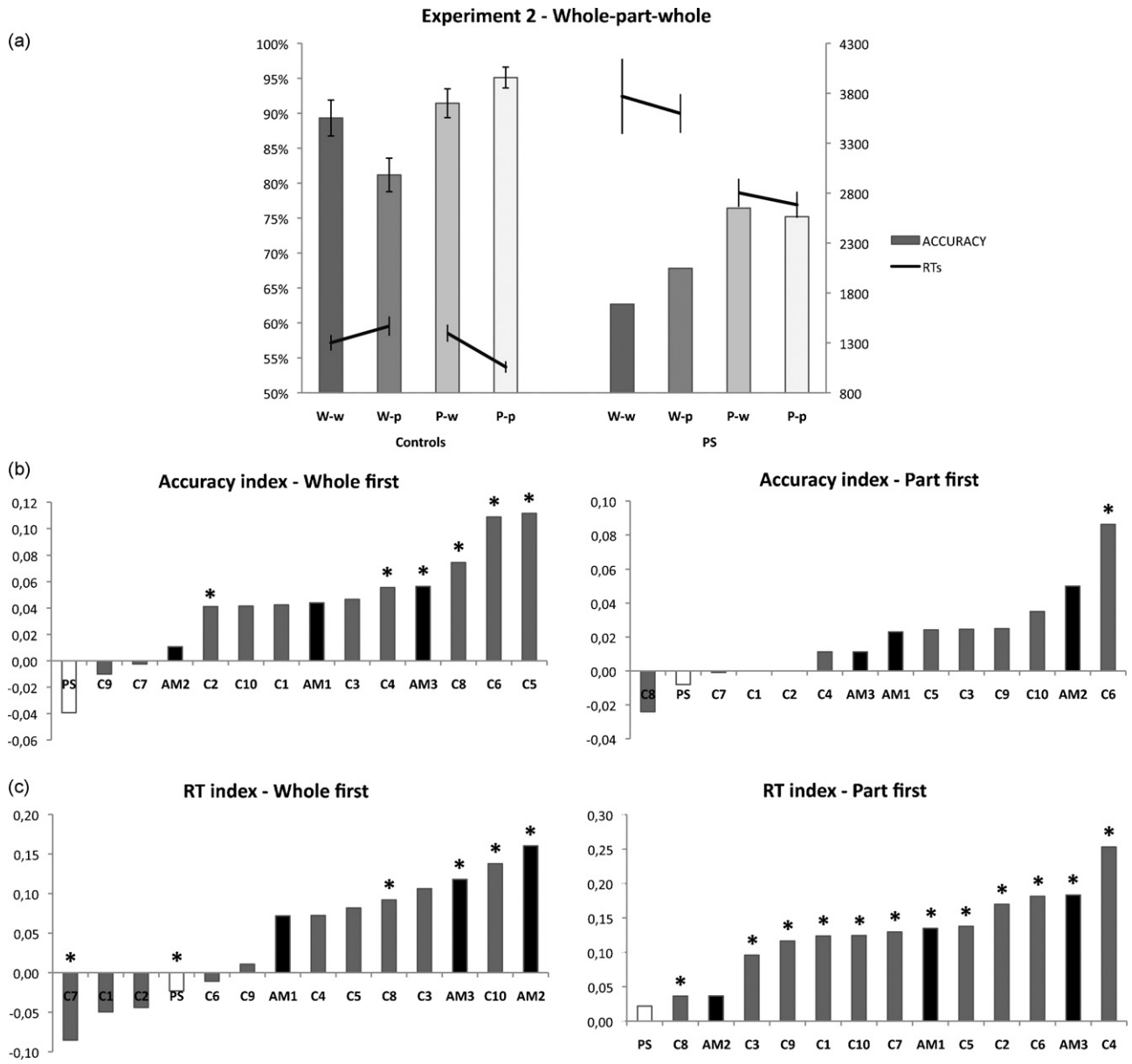

Fig. 3. Experiment 2: whole–part–whole. (a) Performance for normal controls and PS are displayed in the same graph for both accuracy and correct RTs (SE). (b) Accuracy and c. RT indexes were computed separately for trials in which targets were whole faces, or face parts, respectively. The indexes (ranked) represent normalized scores indicating the relative differences between the conditions in which probe stimuli were presented as "parts" or "whole faces", respectively. For accuracy scores, these indexes varied between −.01 and .112 (whole first index), and −.024 and .086 (part first index). For correct RTs, they ranged from −.085 to .16, and .036 to .253, respectively. Asterisks indicate significant differences between both conditions on the single-subject level.

3.4.1.2. Stimuli. Gray-scaled full-front pictures of 20 faces (neutral expression, half male, no glasses/facial hair) were used. The faces (ca. 180 × 230 pixels) were fitted onto a gray background and separated into top and bottom halves by inserting a 1.76 mm gap located 15 pixels above the upper nostril limit. This gap was used to ensure that top and bottom halves could be easily distinguished, even in the aligned condition, as participants were instructed to match "the top part of the face". For each original face the top part was combined with the bottom of another randomly selected one. The lower parts of the resulting faces were then laterally offset to the right until the center of the (bottom part of the) nose was vertically aligned with the contour of the top part. The resulting face pairs for a given original face – differing only with respect to the bottom parts – were used for the "same" condition with aligned and misaligned face halves, respectively (40 pairs in the "same" condition). Examples of the composite stimuli are depicted in Fig. 1b. Furthermore, nine faces were created by combining randomly selected top and bottom parts, and paired with nine of the original faces, again with the face parts being aligned and misaligned as well (18 pairs for the "different" condition which were not considered in the analyses).

3.4.1.3. Procedure. Each trial involved consecutive presentation of two composite stimuli of the same alignment, which had to be judged with regard to the identity of the top part (same or different). Trials commenced with a centrally presented fixation cross (300 ms); after a 200 ms blank, a target face was presented (600 ms) and a probe stimulus appeared after a 300 ms ISI (trials were separated by a 1000 ms ITI). Targets and probes appeared at slightly different screen locations in order to restrict local matching strategies. The experiment consisted of 116 randomly presented trials, with two blocks of equal length (each containing 40 "same" and 18 "different" trials; this bias was equal across conditions and was

introduced as only same trials were of interest (see e.g., Michel et al., 2006). Thus, across the four sessions, there were 160 trials per critical conditions ("same aligned" *vs.* "same misaligned"); with four foregoing practice trials. All participants were tested on a laptop located 60 cm in front of them (17 in., 60 Hz refresh rate; 1024 × 768 pixel resolution). Aligned stimuli subtended 7.4° × 5.4°, misaligned stimuli were 7.4° × 8.1° of VA.

3.4.2. Results

Across all conditions ("same" and "different" trials averaged) PS performed significantly above chance (82%, $p < .0001$). She was however much slower than both AMs ($t(368) = 8.26$, $p < .0001$, and $t(368) = 18.24$, $p < .0001$).

For the control group, a significant advantage for misaligned trials, for which they were generally more accurate, $t(11) = 2.36$, $p = .02$, and faster, $t(11) = 4.9$, $p < .001$ (Fig. 4a).

Comparing PS' composite face indexes ([misaligned-aligned/misaligned + aligned]) to those of controls as a group indicated that neither her accuracy, nor RT indexes differed significantly ($t(11) = .011$, $p = .46$ and $t(11) = 1.16$, $p = .13$). While this result may suggest that PS showed some degree of composite effect, the data analysis at the single-subject level suggest otherwise: only four participants were significantly more accurate for misaligned as compared to aligned trials (all $p < .05$), but not PS (Fig. 4b); for correct RTs however, *all* controls showed an advantage for misaligned trials ($p < .013$), but not PS ($p = .11$), who had the smallest index (Fig. 4c).

3.4.3. Discussion

The group data indicate that normal controls' perceptual judgments of top face parts were detrimentally influenced by task-irrelevant bottoms if the parts were aligned. This composite face effect was absent for PS, and can be interpreted as indicative of abnormal HP. The following experiment was conducted in order to reinforce these observations and to investigate whether these contextual effects could also be observed if matching *bottom* face parts is required.

3.5. Experiment 4: bottom composite

3.5.1. Methods

3.5.1.1. Participants. The control participants were the same as reported in experiment 3; they all completed four sessions of the present experiment in succession. For PS there was a 7-month interval between the first and second, and a 5-month interval between the second and third testing time; the third and fourth sessions were carried out on the same day.

3.5.1.2. Stimuli and procedure. The same gray-scaled full-front pictures as described in experiment 4 were used (see Fig. 1b). The procedure was identical to experiment 3 (stimulus presentation, number of trials per condition, etc.), with the exception that participants were required to make identity judgments of the *bottom* parts.

3.5.2. Results

Across all conditions ("same" and "different" trials averaged) PS performed significantly better than chance (86%, $p < .0001$). She was significantly slower (average RT: 1290 ms) than both AMs ($t(385) = 19.26$, and $t(385) = 22.82$, both $p < .0001$).

The group of controls showed a higher accuracy on misaligned trials ($t(11) = 1.55$, $p = .08$), along with significantly slower RTs ($t(11) = 7.6$, $p < .0001$) as compared to aligned trials (Fig. 5a).

PS' accuracy indexes did not differ from those of controls ($t(11) = .50$, $p = .31$) (Fig. 5b), but for correct RTs there was a trend for a lower index for PS as compared to controls ($t(11) = 1.66$, $p = .06$) (Fig. 5c).

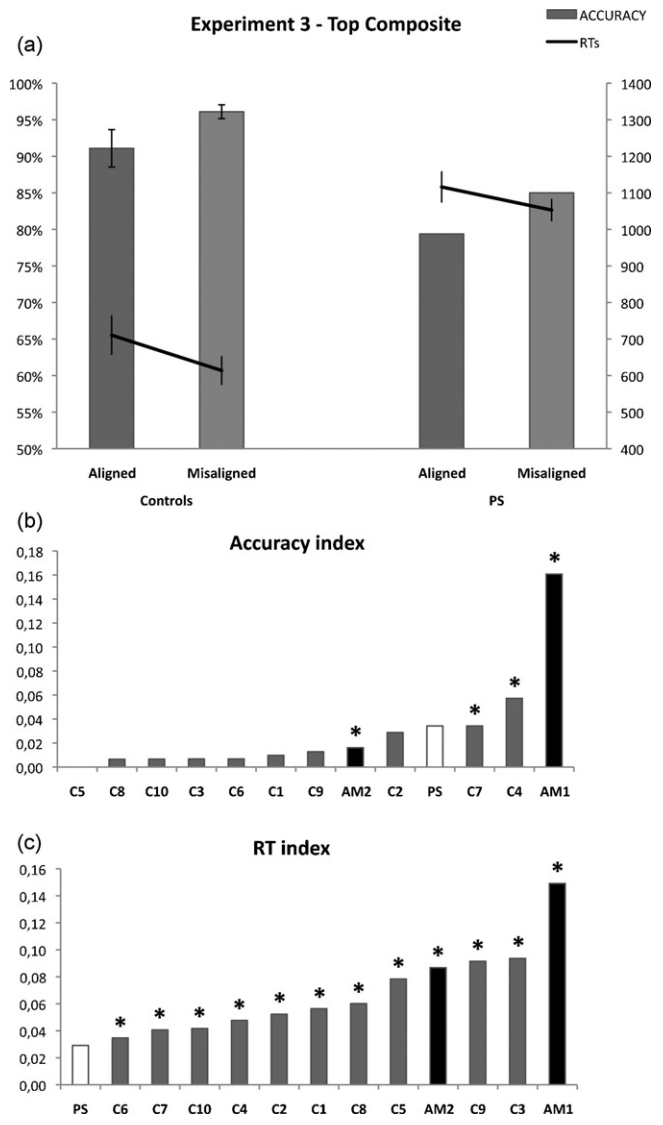

Fig. 4. Experiment 3: top composite. (a) Performance for normal controls and PS are displayed in the same graph for both accuracy and correct RTs (SE). (b) Accuracy and c. RT indexes for each participant (ranked) represent normalized scores indicating the relative differences between conditions in which composite stimuli were presented aligned or misaligned, respectively. For accuracy the indexes varied between 0 and .161, and from .035 to .149 for correct RTs. Asterisks indicate significant differences between both conditions on the single-subject level. While PS appears to be in the normal range with respect to her accuracy index, single-subjects analyses revealed that only 4 controls showed an accuracy advantage for misaligned trials. Analyses of correct RTs revealed that *all* controls showed an RT advantage for misaligned trials, which was not the case for PS, who had the smallest index.

At the individual level, only 3 controls' accuracy scores (including those of AM1 and AM2) were significantly lower for the aligned condition ($p < .05$), and this was not the case for PS ($p = .17$). Regarding RTs, every control participant performed faster on misaligned trials ($p < .05$), PS however did not ($t(260) = .94$, $p = .17$).

3.5.3. Discussion

Although there seemed to be trends for composite effects for PS in this experiment, as in experiment 3, none of these effects were close to reaching statistical significance despite the large number of trials performed, and the significant effects found for each control (with particularly large effects in AM controls).

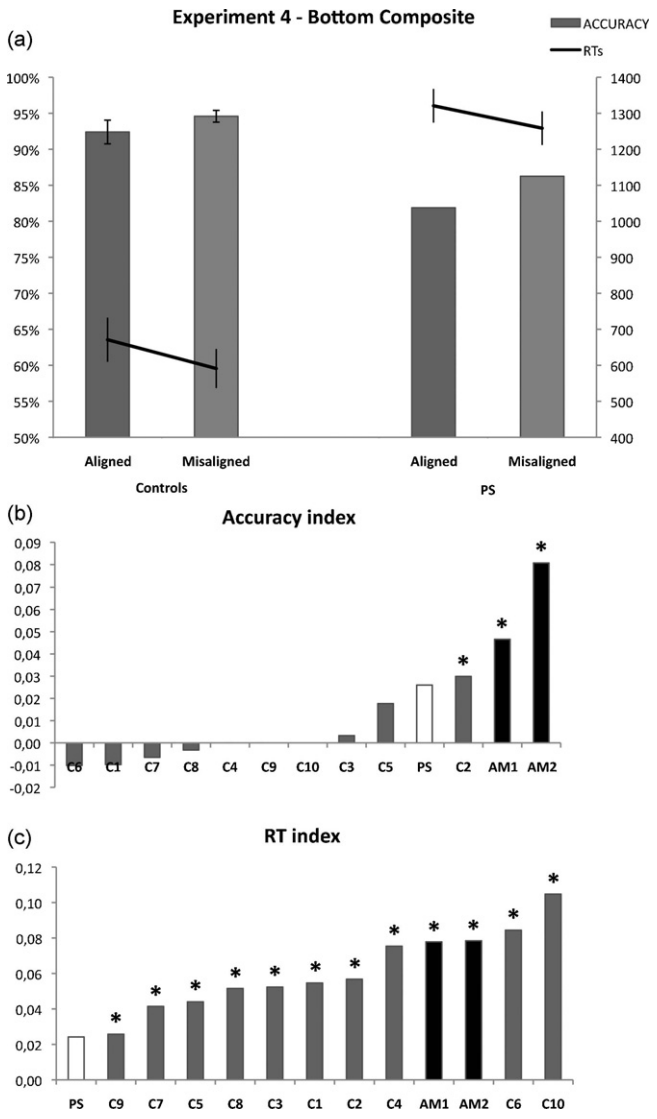

Fig. 5. Experiment 4: bottom composite. (a) Performance for normal controls and PS are displayed in the same graph for both accuracy and correct RTs (SE). (b) Accuracy and (c) RT indexes for each participant (ranked) represent normalized scores indicating the relative differences between conditions in which composite stimuli were presented aligned or misaligned, respectively. The alignment indexes (normalizing overall accuracy and RT differences, see above) for all participants are displayed in Fig. 5. These ranged from −.010 to .081 for accuracy indexes, and .026 to .105 for correct RTs. Asterisks indicate significant differences between both conditions on the single-subject level. Although PS' accuracy index appears to be in the normal range, single-subjects analyses revealed that only 3 controls showed an accuracy advantage for misaligned trials, which was not found for PS. Analyses of correct RTs revealed that *all* controls showed an RT advantage for misaligned trials, which was not the case for PS, who had the smallest RT index.

Again, these observations support the view of her deficit lying at integrating facial information into a holistic percept.

Interestingly also, given her reasonably high performance in this task, a general floor effect cannot account for the absence of a normal composite face effect (her performance on aligned trials was indeed comparable to that of AMs). It is the *absence of a benefit due to misalignment* of face parts that gives rise to her overall performance being inferior to that of both AMs (Figs. 4 and 5).

We note however, that in both experiments 3 and 4 we found non-significant trends for an effect of alignment for the patient PS. We hypothesized that this may reflect a more general effect of alignment of the face parts, rather than "residual" HP, and attempted to address this issue in experiment 5.

3.6. Experiment 5: top composite (alignment × bottom change)

3.6.1. Rationale and hypothesis

In matching tasks the composite face paradigm assesses the influence of one face part on the other, by means of manipulating the irrelevant (e.g., bottom) part's position, thereby measuring the effect of alignment. That is, the effect of changing the *identity* of the irrelevant part is not directly tested, as the bottom parts always differ in the critical trials (those with the same top part). Although this procedure is widely used in the literature (including our own studies), we reasoned that it would be more correct to demonstrate that the effects observed are not only due to a simple effect of alignment of face parts, but also to the fact that this bottom part is *of a different identity* between the two faces. In other words, one would like to demonstrate that judging whether two top parts are the same, is more difficult if they are aligned with *different* bottom parts (as compared to misaligned trials), but not if they are aligned with *identical* ones. Hence, an interaction between identity of the bottom part and the factor alignment, for "same" trials would be anticipated, and reveal a purer measure of the composite face effect.

Thus, here we extended the composite face paradigm by adding another baseline condition in which the bottom part does not change between the two faces matched. The critical condition remains the one in which the observers have to respond "same" for the top parts, which are presented with different bottoms. Both the effect of associating a different bottom part, and that of alignment can be considered in this paradigm, therefore allowing a more complete measure of the composite face effect (as an interaction between bottom change and alignment). In summary, the present experiment included four "same" conditions in which the tops remain the same and the bottoms change (Fig. 1c), as well as two "different" conditions in which the tops change as do the bottoms (aligned/different top and bottom; misaligned/different top and bottom). For "same" trials we expected to obtain an interaction between the two factors *alignment* and *bottom change* (or: bottom identity) for normal controls, but not for PS.

3.6.2. Methods

3.6.2.1. Participants. Besides PS (57 at time of testing), we tested two AMs (57, 61 years) and 10 undergraduate psychology students (age range 19–21); neither of the controls participated in the previous experiments.

3.6.2.2. Stimuli and procedure. For this experiment a new set of 23 full front, color images of cropped faces (neutral expression, 16 female, no glasses/facial hair; ca.160 × 230 pixels) were fitted onto a white background and processed as described above (gap, misalignment). For each original face (same top/same bottom) a second one was created by combining the top with a different bottom part from a randomly selected face (same top/different bottom). For the "same" condition four possible trials were created: the original face was paired with itself (*aligned/same bottom* and *misaligned/same bottom*) and its combined version with a different bottom (*aligned/different bottom* and *misaligned/different bottom*) (Fig. 1c). With respect to the "different" condition, each (mis)aligned face was paired with another, randomly selected aligned one (*different top & bottom* condition). The procedure and instructions were identical to experiment 3. A total of 138 trials were divided into two blocks of equal length (92 "same" and 46 "different" trials, with 23 per condition). The experiment began with 4 practice trials (excluded from analyses). Participants were tested on a laptop located 60 cm in front of them (17 in., 60 Hz refresh rate; 1024 × 768 pixel resolution). Stimuli subtended approximately 7.5° × 5.5° (aligned), and 7.5° × 8.0° (misaligned) of VA, respectively.

3.6.3. Results

PS was overall significantly above chance level (85%, $p < .0001$), but slower (average RT: 1072 ms) than her AMs ($t(158) = 2.77$, $p < .004$, and $t(162) = 1.91$, $p < .03$).

There was a main effect of alignment, $F(1,11) = 34.02$, $p < .001$, and bottom change, $F(1,11) = 11.57$, $p < .006$, on accuracy. Importantly, there was a significant interaction between these factors, $F(1,11) = 13.12$, $p < .005$: when the bottom parts of the faces were identical, there was no effect of alignment ($t(11) = .81$, *ns*), while there was a large effect of alignment when bottom parts differed, $t(11) = 5.31$, $p < .001$.

The exact same results were found for correct RTs: analyses revealed a main effect of alignment ($F(1,11) = 6.03$, $p = .03$) and bottom change ($F(1,11) = 13.00$, $p < .005$), and a significant interaction between the two factors ($F(1,11) = 9.60$, $p = .01$). Again, this interaction was due to an absence of effect of alignment when the bottom parts were identical ($t(11) = .35$, *ns*), but shorter RTs for misaligned trials when bottoms differed, $t(11) = 2.97$, $p = .01$.

Comparing PS' alignment indexes to those of controls for identical bottom parts yielded no significant differences ($t(11) = .22$, and $t(11) = .39$, *ns*, respectively). However, her alignment indexes when the bottom parts were different were significantly lower than normal controls for both measures ($t(11) = 3.20$, $p < .01$, and $t(11) = 2.07$, $p = .03$) (see Fig. 6b and c).

At the individual level, when bottom parts where *same*, none of the participants' accuracy scores (including PS') differed as a function of alignment (all $p > .07$); only three controls' RTs differed across conditions, with two showing longer RTs for aligned trials (C1, C3; $p < .02$) and one demonstrating the opposite pattern (C2; $p = .01$) (see Fig. 6b and c, left). Contrariwise, for trials with *different* bottom parts, controls' performance was better on misaligned trials, either regarding accuracy (C1, C3, C5, C10, $p < .04$; non-significant trends for C8, AM1; $p \leq .09$), or RTs (C8, C9, AM1, AM2, $p \leq .05$; non-significant trends for C3, AM1; $p \leq .07$). This was in sharp contrast to PS, who showed significant effects in the opposite direction (accuracy: $p = .04$, RTs: $p < .01$) (see Fig. 6b and c, right).

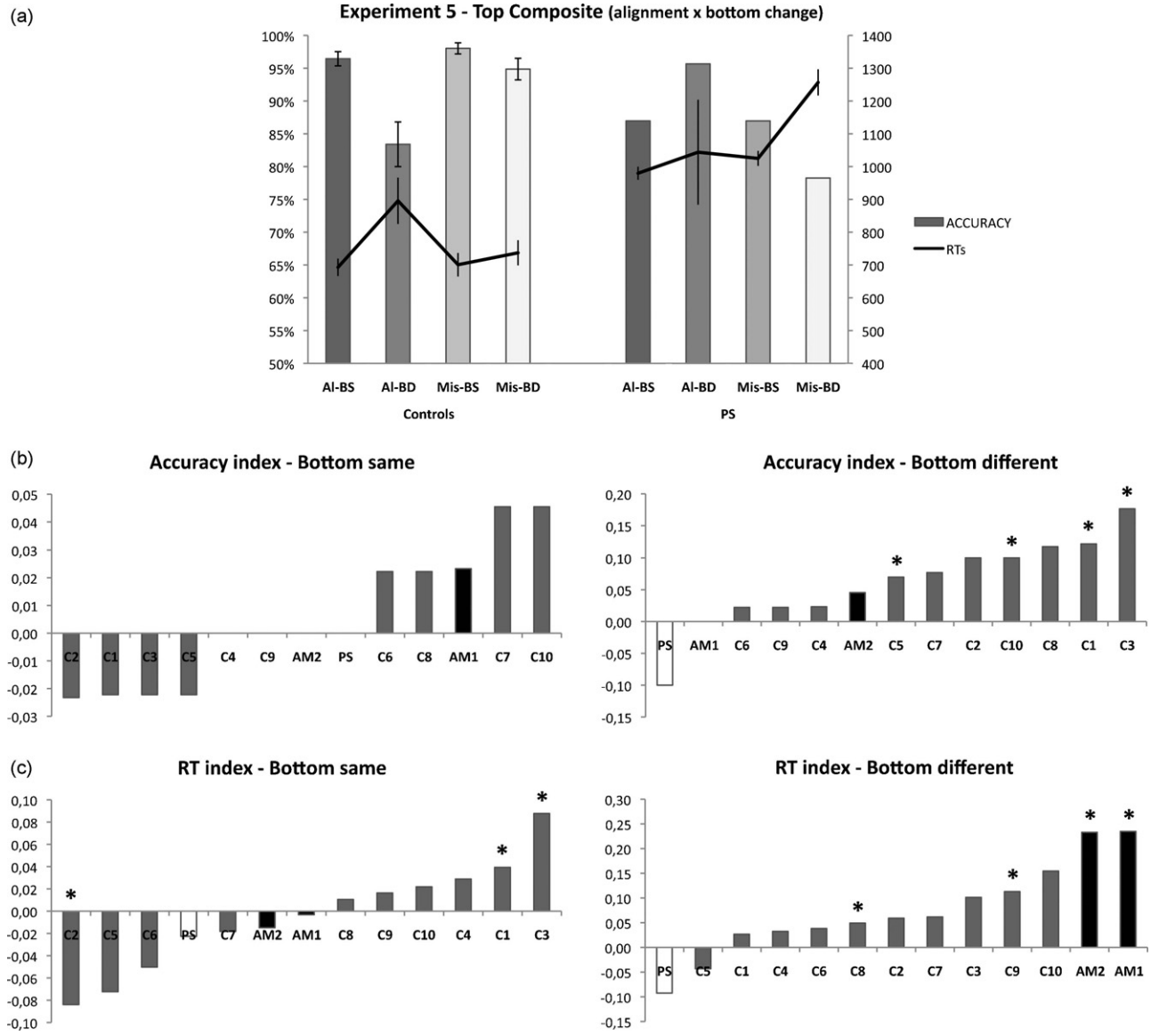

Fig. 6. Experiment 5: top composite (alignment × bottom change). (a) Performance for normal controls and PS are displayed in the same graph for both accuracy and correct RTs (SE). (b) Accuracy and c. RT indexes were calculated separately for trials on which the bottoms were the same (left), or differed (right), respectively. The indexes for each participant (ranked) represent the relative increase in performance due to bottom part misalignment. Accuracy indexes ranged from −.023 to .045 for bottom same trials, and .000 to .176 for bottom different trials; RT indexes ranged from −.084 to .088, and −.043 to .235, respectively. Asterisks indicate significant differences between aligned/misaligned conditions on the single-subject level.

3.6.4. Discussion

The results of experiment 5 replicate and reinforce the previous findings. All controls demonstrated strong composite effects, the largest being observed for the two AMs, who both presented composite effects for RTs. The lack of significant effects for accuracy scores for AMs is not an issue, as AM2 showed a non-significant trend in the predicted direction and there was no evidence of a trade-off with RTs. Contrariwise, PS did not present any interaction between the two factors alignment and bottom change. Second, concerning the trials for which the bottom parts differed, PS was even more efficient (accuracy and RTs) if the two parts were aligned, which is opposite to controls' performance. As the AMs presented, if anything, the largest interference indexes, the absence of an effect for PS cannot be attributed to her age, but appears to truly reflect a lack of HP.

4. General discussion

The goal of the present study was to assess HP in a pure case of prosopagnosia, in order to shed light on the nature of the face processing impairment of AP patients in general. Experiments 1 and 2 assessed HP applying the whole–part paradigm (Tanaka & Farah, 1993), which refers to the greater proficiency at recognizing facial features when embedded in facial context at encoding and recognition stages. In experiment 1, controls benefited from the presence of contextual information for feature recognition. Furthermore, using a full design (experiment 2) they showed a classical whole–part advantage, and were generally less efficient if the format changed across encoding and retrieval stages. These findings, thought to reflect a hallmark of HP (e.g., Tanaka & Farah, 1993; Tanaka & Sengco, 1997; Leder & Carbon, 2005; Michel et al., 2006), were not observed for PS. In experiments 3, 4 and 5 we investigated HP by means of the composite face effect (Young et al., 1987), which refers to less efficient matching/judging of a face part when it is aligned with a task-irrelevant counterpart. The composite effect was found for controls irrespective of whether top (experiment 3) or bottom parts (experiment 4) were judged—but was never observed for PS. These results were replicated using a more complete paradigm (experiment 5), which allowed separating the effect of alignment from that of a change of identity. While all controls presented an interaction between identity and alignment, there was no evidence of such effects for PS. Thus, irrespective of the face part to be judged and the type of composite design used, we failed to find evidence for normal HP in this case of AP.

For several reasons, we believe that the present study provides particularly compelling evidence for a lack of HP in AP. First, many studies that investigated issues related to HP in single cases of AP usually report a single experiment (Farah et al., 1995; Saumier et al., 2001; Sergent & Signoret, 1992b; Barton, Zhao, & Keenan, 2003). However, given the large amount of variability between normal observers, and the fact that significant effects are not found for each control in a given experiment (as illustrated here), we believe that it is important to collect evidence from multiple experiments indicating that the patient does not show any evidence for normal HP.

Second, the sensitivity of each experiment was tested with a group of participants, including a few AMs who also completed a large number of trials per experiment. While one may argue that PS should have only been compared to a group of AMs, we would like point out that the effects found for the age-matched participants were not weaker than the effects found in younger controls considered as single subjects (if anything, the opposite was often found; see Figs. 4–6). Furthermore, when reporting single cases in this area of research it is not uncommon to test only a limited number of AMs, only a single one (e.g., Boutsen & Humphreys, 2002; Bukach, Bub, Gauthier, & Tarr, 2006; Davidoff & Landis, 1990), or none at all (e.g., Levine & Calvanio, 1989; Farah et al., 1995; de Gelder et al., 1998; de Gelder & Rouw, 2000; Marotta et al., 2002, for patient RN; Saumier et al., 2001; Behrmann, Marotta, Gauthier, Tarr, & McKeeff, 2005). Most importantly, the lack of HP effects for PS here cannot be attributed to her overall lower level of accuracy and/or her relatively slower performance as her performance was always well above chance level. Furthermore, lower accuracy or slower performance overall does not preclude the observation of effects. As a matter of fact, the AMs showed equally large or even larger effects than (the more efficient) younger controls in all experiments.[2]

These observations of a lack of HP in PS, a pure case of AP, have several theoretical implications for our understanding of AP and normal face processing.

As indicated above, abnormal inter-dependence between facial features in AP has been reported for a number of cases, and thus apparently represents a common deficit. Other, indirect evidence is provided by reports of abnormal face inversion effects (e.g., Farah et al., 1995; Gauthier et al., 1999; Marotta et al., 2002; Delvenne et al., 2004), as well as impaired perception of inter-feature distances (Barton et al., 2002; Joubert et al., 2003), in particular if not informed about the nature and location of the diagnostic cue (indicative of a type of HP impairment; Ramon & Rossion, 2009).

Thus, although previous evidence for impaired HP in AP could be more solid in our opinion, it appears that despite different lesion localization, etiologies and associated deficits (Sergent & Signoret, 1992a,b; Schweich & Bruyer, 1993), many AP patients present impairments of HP. To our knowledge, only three cases have been reported to show normal HP and would thus pose exceptions to this view: PV (Sergent & Poncet, 1990), PC (Sergent & Signoret, 1992b) and LR (Bukach et al., 2006). While it is possible that these three patients process individual faces holistically, a complete absence of any HP impairment in these cases of AP remains debatable, for several reasons. First, the evidence is based on a single experiment (with unconventional paradigms and analyses) in each case, and should therefore be completed with mores solid evidence collected from multiple experiments.[3] Second, there is in fact evidence for abnormalities of HP for the patient LR. He has been described as unable of considering multiple features of a face altogether, focusing on the mouth at the expense of the eyes, or vice-versa (Bukach et al., 2006), and can also show slow processing of inter-feature distances as compared to local feature changes—a pattern which can be interpreted as a malfunctioning holistic face processor (Rossion et al., 2009; Ramon & Rossion, 2009). Considering this, we suggest that the more sensitive measures of HP as employed here, ought to be applied to other cases of AP, such as LR. While it is possible that this patient would indeed present a residual ability of processing individual faces holistically, we would predict that his processing of faces is also characterized by a reduced holistic processing mode. Such an investigation would provide an answer to the question whether the deficit characterized here for PS can be ubiquitous in all cases of AP, at least to some degree.

Finally, one may ask how patients with different lesion localization might all show a common functional impairment at integrating

[2] Both developmental and pathological investigations have also reported strong HP effects despite the lower performance level and prolonged response times of populations investigated (4–10 year olds: Tanaka et al., 1998; de Heering et al., 2007; autistic subjects: Nishimura et al., 2008).

[3] Patients PV and PC were tested in an individual matching task of faces differing with one or multiple features (Sergent, 1984), showing interactivity among the features to reach a decision. Normal HP for the patient LR was also concluded based on a single experiment, using a paradigm similar to the composite face paradigm but with the two halves of the face presented at encoding, followed by a cue indicating which face half has to be processed. The authors measured a congruency effect by mixing different and same trials in the analysis, and showed that the patient LR's congruency effect did not differ from a few normal controls (Bukach et al., 2006).

features into a global, individual face representation. One reason may be that damage to any node of the underlying distributed cortical face processing network (Sergent & Signoret, 1992b; Haxby, Hoffman, & Gobbini, 2000) impinges on the functional integrity of other areas of this network (Fox, Iaria, & Barton, 2008; Rossion, 2008b). Thus, in all AP patients, a common critical aspect of face processing – holistic face perception – could always be altered, at least to a certain extent.

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