

All new kids on the block? Impaired holistic processing of personally familiar faces in a kindergarten teacher with acquired prosopagnosia

Meike Ramon¹, Thomas Busigny², Frederic Gosselin³, and Bruno Rossion^{2*}

¹University of Fribourg, Department of Psychology, Fribourg, Switzerland, ²University of Louvain, Psychological Sciences Research Institute and Institute of Neuroscience, Louvain-La-Neuve, Belgium, ³Université de Montréal, Département de psychologie, Montreal, Canada

Acquired prosopagnosia is primarily defined as a defect in recognizing familiar faces. Nonetheless, for practical and methodological reasons, studies of such rare patients typically use pictures of unfamiliar faces. Here we report an extensive investigation (17 behavioral tasks grouped in 9 experiments) with a homogenous set of personally familiar faces in PS (Rossion et al., 2003), a well-documented case of acquired prosopagnosia with intact object recognition. PS's recognition of the face pictures of 3-4 year-old children of her kindergarten is severely impaired – both in terms of accuracy and speed of recognition – and differs qualitatively from her colleagues' performance. Relative to these typical individuals, PS relies more on external features, color and local details of faces. She is also specifically impaired at processing the eye region in 2-alternative face matching tasks, as well as in a familiar face recognition task performed both with pre-defined isolated parts and with randomly placed apertures revealing selective parts ("Bubbles", >20.000 trials) of the personally familiar faces. These observations indicate that the same impairment observed previously with unfamiliar faces for PS and other cases of acquired prosopagnosia is associated with a deficient long-term representation of the eye region. Various manipulations that differentially affect the processing of the eye region suggest that this impairment is a consequence of the inability to represent the multiple parts of the eye region, and of the whole familiar face, as a single unit. This impairment in holistic processing is further evidenced here across different paradigms with composite faces, wholes and parts, and configurally distorted faces, mirroring and strengthening previous observations made with unfamiliar faces in PS and other cases of acquired prosopagnosia. Altogether, these observations suggest that prosopagnosia following brain damage affects unfamiliar and familiar face processing in a qualitatively similar way.

Key words: acquired prosopagnosia; face recognition; personal familiarity; holistic representation

Introduction

Recognition of people from their face is one of the most important functions of the human brain, supported by a large network of cortical areas. Damage to this network can lead to a severe impairment in face recognition, i.e. (acquired) prosopagnosia (Quaglino, 1867; Bodamer, 1947, Hecaen & Angelergues, 1962; for more recent cases see e.g., Sergent & Signoret, 1992; Barton, 2008a; Busigny et al., 2010a; see Davies-Thompson et al., 2014; Rossion, 2014 for reviews). In rare cases, the visual recognition impairment in prosopagnosia is strictly limited to faces: object recognition is preserved (e.g., Henke et al., 1998; Riddoch et al., 2008; Busigny et al., 2010a; see the last reference for a tentative list

of such patients and a review), individual exemplars of non-face objects can be individualized accurately and rapidly (Busigny et al., 2010a; 2010b; 2014), and novel non-face objects can be learned at the individual level (Rezlescu et al., 2014). Since behavioural performance of these patients is not affected by general difficulties at processing object shapes, these rare cases of "pure prosopagnosia" can be particularly informative regarding the nature and neural basis of acquired prosopagnosia, and thus of typical face recognition processes in humans.

Over the past decade, the behavior and neurofunctional responses of such a case of acquired pure prosopagnosia, the patient PS (first reported in Rossion et al., 2003) has been extensively documented, following the rationale of the single-case approach in

neuropsychology (Caramazza, 1986; Shallice, 1988). At the neural level, the study of PS has provided information concerning the neurofunctional organization of the cortical face network. Specifically, PS exhibits face-selective activation in the lateral section of the right middle fusiform gyrus (“fusiform face area”, FFA) despite damage to the ipsilateral inferior occipital gyrus (IOG) and no “occipital face area” (OFA) (e.g., Rossion et al., 2003; Schiltz et al., 2006). These findings have inspired a series of studies with other patients and neuroimaging paradigms in the healthy brain (e.g., Steeves et al., 2006; Jiang et al., 2011) that have led to the reformulation of the conventional hierarchical view of face processing in the human brain (Haxby et al., 2000; Rossion, 2008; Duchaine & Yovel, 2015).

At the behavioral level, among other observations, an experiment involving the response classification method “Bubbles” (Gosselin & Schyns, 2001) demonstrated that PS relies much more on the mouth than the eyes when processing faces (Caldara et al., 2005). This finding provided objective – i.e. with an unbiased predefinition of facial information – support for the early hypothesis that acquired prosopagnosia is associated with deficient processing of the eye region of the face (Gloning & Quatember, 1966; Gloning et al., 1966). Since then, this atypical behavior has been observed in several cases of acquired prosopagnosia tested with face matching tasks (Bukach et al., 2006; 2008; Barton, 2008b; Busigny et al., 2010; 2014; Pancaroglu et al., 2016).

PS’s reduced reliance on the socially crucial eye region (for a review see Itier & Batty, 2009) was initially attributed to a loss of holistic face perception, i.e. the ability to process the parts of a face as an integrated unit (Caldara et al., 2005). The reasoning is that a holistic processing defect forces the prosopagnosic patient to analyze each part of a face in turn, i.e. analytically; in these conditions, the eye region, constituted of several different elements, loses its

diagnosticity. This proposal has been supported by PS’s fixations being located exactly on the mouth and each eyeball (Orban de Xivry et al., 2008), rather than centrally on the top of the nose as found for typical observers (Peterson & Eckstein, 2012). Subsequent studies using various stimulus manipulations and gaze-contingent paradigms confirmed that the patient PS does not represent individual faces holistically (Ramon et al., 2010; Van Belle et al., 2010; 2015), as in other cases of acquired prosopagnosia with variable lesion locations (e.g., Levine & Calvanio, 1989; Sergent & Villemure, 1989; Spillmann, et al., 2000; Barton et al., 2002; 2003; Boutsen & Humphreys, 2002; Riddoch et al., 2008; Busigny et al., 2010b; 2014; Van Belle et al., 2011).

However, with few exceptions (Orban de Xivry et al., 2008; Busigny & Rossion, 2010, Experiment 5; Van Belle et al., 2010b, one gaze-contingent experiment in a preliminary report), all of these studies of the prosopagnosic patient PS were performed with pictures of *unfamiliar* faces. In fact, to our knowledge, besides basic clinical evaluation using famous faces to confirm an impairment of face recognition and examine nonconscious (“covert”) recognition (e.g., Bobes et al., 2003; Bruyer et al., 1983; de Haan et al., 1987, 1991; Diamond et al., 1994; Dixon et al., 1998; Barton et al., 2001; Liu et al., 2014; Schweinberger & Burton, 2003 for a review), most of the investigations performed with cases of acquired prosopagnosia have used pictures of unfamiliar faces in matching/discriminating tasks, or old/new recognition tasks. Some studies report difficulties in personally familiar face recognition, either based on patients’ or relatives’ reports, or tests administered in the realm of the general neuropsychological assessment (e.g., Malone et al., 1982; Bruyer et al., 1983; Sugimoto et al., 2012; Bala et al., 2015; Bate et al., 2014). Also, only a few studies have addressed the neurofunctional processing of personally familiar faces in neuropsychological single cases (e.g. Wada & Yamamoto, 1991; Mundel

et al., 2003; Bobes et al., 2004). However, these latter studies vary in terms of the number of stimuli used, as well as the manipulations these stimuli are subject to (e.g., exclusion or availability of external information). More importantly, no study so far has provided a detailed investigation of personally familiar face processing in acquired prosopagnosia with behavioral paradigms typically used to assess unfamiliar face processing.

Arguably, unfamiliar faces offer many advantages in terms of the number of stimuli that can be used and of experimental control in general: a large number of different, yet homogenous face pictures can be used, and these pictures can be further controlled for e.g. age variation and image quality. These unfamiliar face images can be transformed in various ways and presented to the patient and healthy controls, who do not vary in terms of prior knowledge with the stimuli presented. However, the primary complaint of patients with prosopagnosia is their difficulty, often complete inability, at recognizing *personally familiar faces* in their social environment, or at least at distinguishing between unfamiliar and familiar people based on their face (Hecaen & Angelergues, 1962; Benton, 1980). This is because personally familiar face recognition, while being a highly relevant social task that is performed on a daily basis, can be extremely challenging from a computational perspective: one out of a vast number of previously encountered individuals has to be identified despite a number of potential changes in appearance. In light of these considerations, it would be highly informative to systematically evaluate personally familiar face processing in a patient with acquired pure prosopagnosia.

On the one hand, such an investigation could provide support to, or perhaps rather challenge, the conclusions reached by studies of prosopagnosia performed using unfamiliar faces (Benton, 1980). For instance, deficient processing of information conveyed by the eye region has been reported in the context of matching/discrimination of unfamiliar faces (Gloning & Quatember, 1966; Bukach et al.,

2006; 2008; Barton, 2008b; Busigny et al., 2010), as well as those learned through photographs (Caldara et al., 2005). However, whether the eye region of familiar faces is underrepresented in long-term memory by patients with acquired prosopagnosia remains unknown. Moreover, whether personally familiar faces are encoded as a collection of independent parts rather than as holistic representations is also unclear.

On the other hand, testing personally familiar face recognition in a case of acquired pure prosopagnosia whose behavior with unfamiliar faces is already well documented may provide valuable information regarding the issue of whether familiar and unfamiliar faces are processed in a qualitatively different way (Tong & Nakayama, 1999; Burton & Megreya, 2006; Megreya & Burton, 2006; Megreya & Burton, 2007; Johnston & Edmonds, 2009; Burton, 2013). Since familiar faces can be activated through multiple sources of information, they can be recognized across even extreme viewing distances (Ramon, 2015) and considerable periods of time (Bahrick, Bahrick, & Wittinger, 1975), and they enable efficient matching of identity across image variations that impede upon unfamiliar face processing (e.g. image resolution, viewpoint; Bruce, 1994; Bruce et al., 2001; Burton, et al., 1999; for personally familiar faces, see Ramon, 2015a,b; Ramon & Van Belle, 2016; Pachai, Sekuler, Bennett, Schyns & Ramon, 2016; Goffaux & Greenwood, 2016; Goffaux & Dakin, 2010). However, whether holistic face processing, which is critical for individualization, differs qualitatively for personally familiar and unfamiliar faces, remains unknown.

To address these issues, the present study reports the results of an extensive series of experiments using personally familiar faces performed with the prosopagnosic patient PS. Critically, we used faces of individuals that PS not only encountered in everyday life, but that she was forced to learn and recognize professionally. Despite sustaining brain damage in 1992, which caused her pronounced

and long-standing deficit in face recognition, PS had remained very active socially and professionally, having developed strategies to cope with her impairment. Specifically, she worked as a kindergarten teacher for her entire professional career, with only a two-year interruption after her traumatic accident (1992-1994), before retiring three years ago. This unique situation, together with the willingness of her only two colleagues (one age-matched) to participate in behavioral testing, provided us with the opportunity to investigate a case of acquired prosopagnosia and healthy controls using the same set of highly personally familiar faces: the faces of 27 kindergarten children (3-4 years of age), whom they had known for about a year at the time of testing.

Compared to famous faces or the few personally familiar faces that are sometimes used to test prosopagnosic patients, the stimulus set used here offers many advantages in terms of richness and experimental control. It includes high quality pictures of many individuals of the same age, and offers a highly homogenous and controlled set of faces that can be carefully manipulated in terms of the facial information presented. The results of an experiment involving registration of eye movements with these children's faces have been previously reported (Orban de Xivry et al., 2008): when attempting to recognize the children's faces, PS sampled the mouth relatively more than the eyes, and avoided the typical landmark fixation on the top of the nose of the face (Peterson & Eckstein, 2012). Judging whether a child's face was familiar or not, she exhibited very low performance and no inversion effect (Busigny & Rossion, 2010, Experiment 5: 60% vs. 52% for upright and inverted face familiarity decisions), already suggesting that her holistic processing deficit affects processing of both unfamiliar and familiar faces. Furthermore, replicating previous observations with unfamiliar faces (Van Belle et al., 2010a), PS showed a relatively increased impairment at recognizing a familiar face child with a gaze-contingent

mask, as compared to a gaze-contingent window (brief report, Van Belle et al., 2010b).

To summarize, here we report an extensive series of experiments in which we investigated the nature of the information used (or not) by PS and her colleagues when attempting to recognize or identify personally familiar children's faces. We first tested PS's ability to recognize the identity of the personally familiar children from their face pictures, either with full (experiment 1) or degraded information (experiments 1 and 2). Even though PS's ability to discriminate these children faces from unfamiliar faces is close to chance level (Busigny & Rossion, 2010, experiment 5), we expected much better performance with a *constrained* set of stimuli, since the patient was fully aware that *only* the faces of the kindergarten children would be presented. We also conducted two experiments involving a response classification technique ("Bubbles", Gosselin & Schyns, 2001; experiment 3) or constrained stimulus manipulations (isolated parts, experiment 4) in order to test whether PS also presents with a specifically deficient representation of personally familiar faces' eye region. Additionally, we tested classical paradigms of holistic face processing that are usually performed with unfamiliar face pictures (composite face effect, Young et al., 1987; experiment 5; whole-part advantage, Tanaka & Farah, 1993; experiment 6), and two original tests developed for this unique material (shuffled face parts, experiments 7; face geometry effect, experiment 8). A last experiment (9) was motivated by the view that holistic processing can be applied to the entire face, as well as to individual face regions or parts (Rossion, 2013), attempting to relate this processing impairment to the deficiency in representing the eye region.

Materials and Methods

The Patient PS

PS's case has been described extensively in previous publications. Her performance at standard clinical and neuropsychological tests of visual perception and recognition is reported

in Table 1 of Rossion et al. (2003) and Sorger et al. (2007). Her behavioral performance at matching unfamiliar faces and objects (e.g., Busigny & Rossion, 2010; Busigny et al., 2010), as well as neuroimaging results (e.g., Rossion et al., 2003; 2011; Caldara et al., 2005; Schiltz et al., 2006; Sorger et al., 2007) have been reported in many studies, and thus will only be summarized briefly here. PS is a 66 year-old female (born in 1950; 55 and 56 years of age at the time of testing), who sustained a severe closed head injury in 1992. Structural scans revealed extensive lesions of the left mid-ventral (mainly fusiform gyrus) and the right inferior occipital cortex, with minor damages to the left posterior cerebellum and the right middle temporal gyrus (see Sorger et al., 2007 for detailed anatomical data). Despite these multiple, partially extensive brain lesions and the initially pronounced cognitive associated deficits, PS recovered extremely well after medical treatment and neuropsychological rehabilitation (Mayer & Rossion, 2007). Her only continuing complaint concerns her profound difficulty at recognizing faces, including those of family members, as well as her own. To determine a person's identity, she usually relies on contextual information and non-facial cues such as the person's voice, posture, or gait, etc. However, she may also use sub-optimal facial cues such as the mouth, or the external contour of the face (Caldara et al., 2005). The Benton Face Recognition Test (BFRT, Benton & van Allen, 1972) ranks her as highly impaired (score as tested in 2006: 72.2%, significantly below normal controls; 64.81% as tested in 2015 in an electronic version recording RTs: 39.14s per panel, for a total of 14.3 min to perform a test routinely performed in 3 to 7 minutes by normal participants). She is also impaired at the Cambridge Face Memory Test (CFMT, Duchaine & Nakayama, 2006): tested in 2010, PS scored 33/72, a score that is below that of typical subjects, even when correcting for age (i.e., $Z = -2.13$, $p < .05$, using the correcting factor of Bowles et al. (2009); no age-matched

participant tested in that study scored as low as PS).

Her impairment with faces seems largely limited to processing of facial identity. Note, however, that despite her lack of complaints concerning recognition of facial expressions in real-life situations, she performs slightly lower than typical individuals at facial expression categorization with static – but not dynamic – stimuli (Rossion et al., 2003; Richoz et al., 2015). PS's color vision is in the low normal range (Sorger et al., 2007), and she does not present any difficulty in recognizing objects, even at a subordinate level (Rossion et al., 2003a; Schiltz et al., 2006; Busigny et al., 2010). Her visual field is almost full (with exception of a small left paracentral scotoma; see Sorger et al., 2007), and her visual acuity at the time of testing was good (0.8 for both eyes as tested in August 2003).

PS has always worked in a kindergarten, and had worked half time since her accident (2½ days a week, throughout the entire year, with exception of the summer holidays, in July and August). Each year PS supervised about 30 children, separated into two groups (attending the kindergarten in the mornings, or afternoons, respectively). Her ability to recognize these children in the context of the kindergarten is good; in fact her deficit was unnoticed with the exception of one or two occasions, where she mistook a child from another kindergarten for one of the children she was in charge of (i.e., a false alarm). Inside the constrained environment of the kindergarten, she claims to rely on multiple cues to identify the children of the kindergarten, such as their voice, body shape, size, gait, behavior ..., but also external and internal face features. She also reports that these strategies require constant concentration and focusing on the children's physical characteristics, including their face.

Control subjects

All control subjects were female and right-handed. At the time of testing control C1 was 58-60 (i.e., age-matched to PS), and control C2 was 28 and 29 years old. These two controls

were PS's only colleagues, and worked in the kindergarten on a full-time basis. Strictly speaking, they were thus exposed relatively more often to the children's faces than PS, during the 8-9 months preceding the testing. However, in this natural learning and familiarization context, the level of attention on the children's faces is uncontrolled. In fact, PS - fully aware of her impairment - always reported that she had to spend much more time than her colleagues to pay attention to and memorize the children's physical characteristics, including their faces, in order to avoid recognition failures. The required constant high level of concentration was the very reason she worked only half time in the kindergarten after her accident. Interestingly, we also had the opportunity to run some of the experiments with a third control (C3, 35 years old), the mother of one of the children, who substituted PS or her colleagues a couple of times throughout the year (1 full week in October 2005, 6 months before testing, a few days here and there) and was thus much less familiar with the children than PS. No formal testing of face processing impairments was performed with PS's controls. Note, however, that they were fully aware of PS's deficit and - unlike developmental prosopagnosics, who become aware that prosopagnosia represents a clinical impairment - they never reported having difficulties with face processing. Furthermore, given their professional activity and based on their interaction with the authors, we would rule out any other social-affective deficits, such as autism.

Testing sessions

PS was tested over three consecutive days (2h sessions) in May 2006, at the end of the school year (which started in September 2005). C1 and C2 were tested over two days a few weeks later (June 2006), and complementary testing was performed two months later both for PS and her controls (August 2006). C3 could only be tested for a 2h session in June 2006. Data for a small number of subtests (experiments 9a-e) were acquired in August 2007 after refreshing PS's memory with the full face

pictures. For experiment 3 ("Bubbles") we were only able to test PS (tested in 2007-2008; aged 56-57) and C1 (aged 60; tested a few months later for practical reasons). Both were presented with a refresher test of the children's faces before every Bubbles experiment.

General Methodological Aspects

High quality full-front photographs of 27 of the 30 children who were present when taking the pictures (17 females; 3-4 years of age) were taken for experimental purposes only, and with the agreement of the director of the kindergarten. With exception of the pictures of six children (the parents of which provided written consent for publication) these photographs cannot be reported in the present paper. The photographs were used for all experiments, and were modified depending on the specific requirements of a given experiment. For experiment 6 (testing the whole-part advantage), we also used photographs of 9 unfamiliar children of the same age (6 females), taken in a German kindergarten. The proportion of male and female faces differed only slightly between the un-/familiar unfamiliar children, even though the sex of a face was particularly difficult to ascertain given removal of external features (see Figure 1a). When possible, we used color images; gray-scaled stimuli were used in a subtest of experiment 1 (identification), as well as for the composite face paradigm (experiment 5), and some subtests of experiment 9. Some of the experiments reported here required verbal identification of a single stimulus (i.e. naming of whole faces, face parts or features, respectively), with no available cues (or correct assignment of one of the 27 names to a given face stimulus; Experiment 1). The remaining experiments involved 2-alternative forced-choice (2AFC) decisions: either recognition in terms of (a) correct name assignment (two faces preceded by, or presented simultaneously with a name above), or (b) familiarity decision. These 2AFC experiments were particularly important to ensure that PS's performance was well above chance level, in order to allow

comparisons between experimental conditions, as well as analyzing response times (RTs) along with accuracy as dependent variables. The drawback of such a procedure is that control subjects often performed at ceiling for these tasks, with effects more likely to arise in terms of correct RTs. In line with the procedure adopted in our previous investigations of brain-damaged patients, PS was never tested under conditions of stress (i.e., limited time to respond); throughout all experiments stimulus presentation duration was terminated by participants' response. Because of the small number of controls testable with the present experiments, each experiment included a fairly large number of trials, in order to perform statistics at the single-subject level. Some of the experiments were performed several times with small variations (e.g., composite face effect, experiments 5a-d) to strengthen the observations made, in line with a single case approach. All subjects were tested on the same laptop computer, over 2h sessions. Additional sessions were necessary for PS given her slower responses across all experiments. For experiments completed by *three* controls, their results were considered as a control group to compare PS's performance against using a modified t-test to compare brain damage patients to a small set of controls (Crawford & Garthwaite, 2002). We further applied Crawford and Garthwaite's (2005) Revised Standardized Difference Test (RSDT) to test for differences between PS's performance between experimental conditions by comparing her pattern of performance to the differences observed in the control sample. When accuracy data and RTs were analyzed for each individual subject, χ^2 tests of proportions and ANOVAs, or t-tests were performed. For experiments completed by only two controls, single-subject analyses determined the effect of the experimental manipulations applied. Note that, with the exception of experiment 4, correct RTs were analyzed throughout to determine the impact of experimental manipulations on observers' performance. However, in some figures we opted to *display* normalized RTs or

RT indices. This was done because PS was often slower than controls, and we wanted to use the same scale to demonstrate the observed differences associated with the experimental manipulations employed. Note that average correct RTs (and standard deviations), are provided alongside accuracy scores in the respective Tables accompanying the respective experiments.

Experiment 1: Familiar Face Identification

Rationale

PS and her colleagues were first tested using simple identification tasks to assess and confirm their knowledge of the personally familiar faces. Obviously, we expected that the prosopagnosic patient PS would make a large number of mistakes in a task that requires identification of 27 individual familiar faces. However, the participants were aware that all faces in the set were children of the kindergarten (i.e., no unknown faces as distractors, which makes it particularly difficult for PS; see Busigny & Rossion, 2010, Experiment 5), thereby effectively constraining their search for the correct identity. Moreover, Experiment 1a included faces with all external features and even the clothes that the children wore when the pictures were taken. This was done in order to ensure that PS' ability to recognize the children was sufficiently good to perform the experiments reported in this paper. Experiment 1b presented the faces without external features and color information, in order to test the diagnosticity of these cues for familiar face recognition in acquired prosopagnosia.

Stimuli and Procedure

The experiment was carried out using the original color pictures, which conveyed cues involving both hair and clothes, followed by a second test with gray-scaled images without external features (Figure 1a). Subjects were shown each familiar face stimulus in the center of the screen (~250 x 300 pixels at 72dpi for original pictures; 180x220 pixels for cropped pictures; about 3.5°x4.3° of visual angle, VA) together with a list of the 27 names presented

as a column on the left side of the stimulus (Figure 1b). Using the mouse cursor, they had to indicate the name corresponding to the individual presented. After a response was provided the next stimulus was immediately presented. Mistakes were indicated by a red bar crossing the entire screen (i.e., feedback on a trial-by-trial basis). For both identification experiments (presentation of original pictures, and gray-scaled cropped stimuli), each child's photograph was presented twice, resulting in a total of 54 trials. Order of presentation was fully randomized; stimuli were presented using Matlab 6.5 (accuracy and RTs recorded).

Results

The results of Experiment 1 are depicted in Figure 1c and Table 1. With the original photographs, the controls were almost flawless, except for C3, who made 5 mistakes out of 54 trials (91% correct). PS's recognition rate was good (87%, not significantly different from controls, $t=1.73$, ns), but she was much slower than the three controls ($t=7.55$, $p<.01$). Controls were not significantly slower due to removal of color information and external features (C1: $t_{99}=-2.39$, $p<.02$, i.e., shorter RTs for grayscaled, cropped stimuli; C2: $t_{102}=.56$, ns ; C3: $t_{93}=.42$, ns). However, PS's

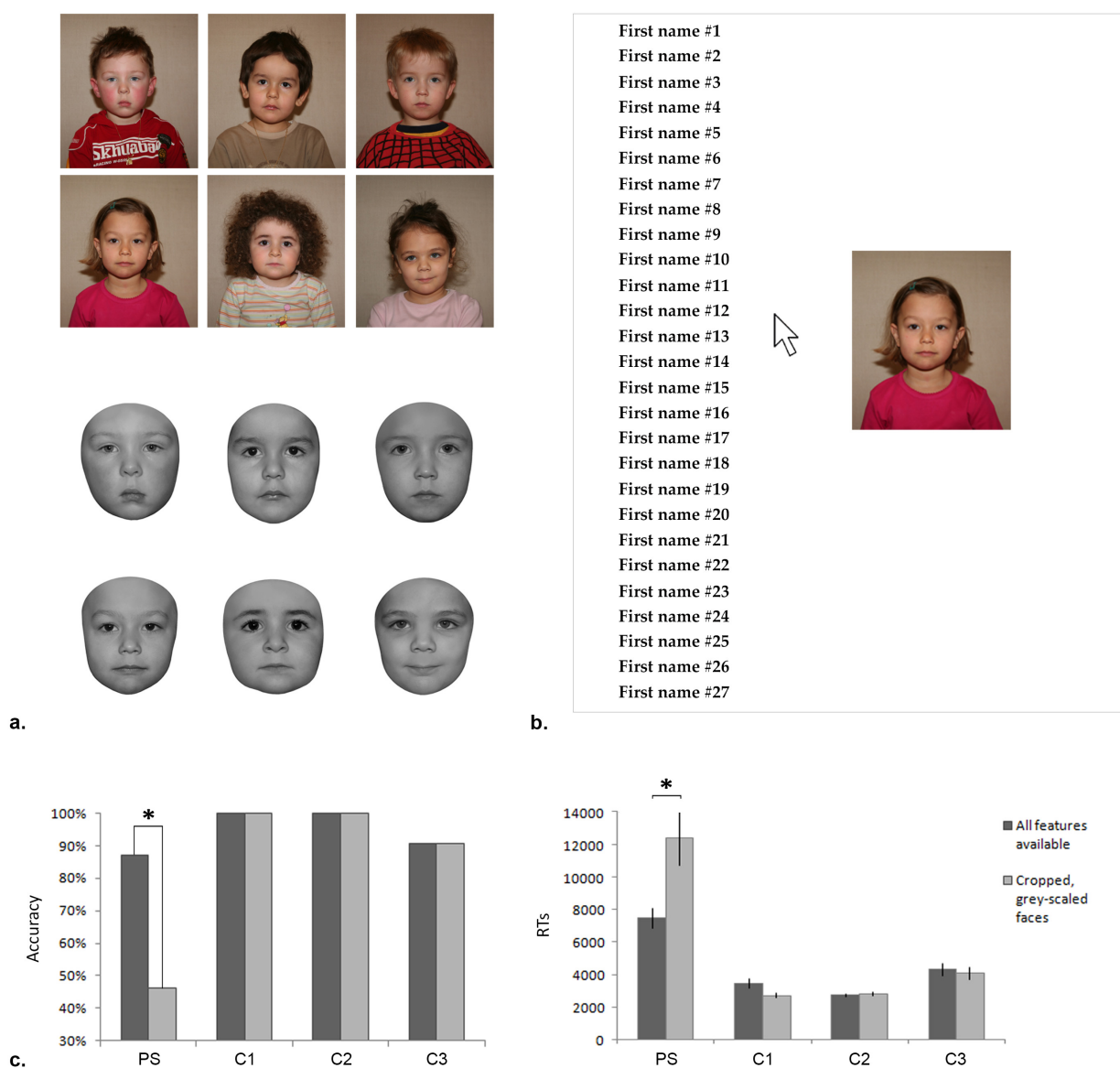


Figure 1. Stimuli and results for Experiment 1: Familiar Face Identification. **a.** Stimuli presented could involve colored full face stimuli including external features (top), or cropped gray-scaled faces (bottom). **b.** Experimental design during familiar face recognition (here with an example of a full-face stimulus). Participants used the cursor to indicate which name corresponded to the child displayed. **c.** Accuracy scores and RTs (with standard errors) for both types of stimuli presented.

performance dropped dramatically for faces presented without external features or color ($t_{68}=3.29$, $p<.005$): her score was below 50% for grey-scaled, cropped photographs (chance level=3.7%), a score which was significantly worse than controls ($t=8.83$, $p<.01$). Again, she was also much slower than controls ($t=7.36$, $p<.01$).

Discussion

Experiment 1 served as a benchmark to demonstrate that, despite being prosopagnosic, PS is able to identify the personally familiar faces on full photographs, with unlimited time, and to ensure that all controls knew the children sufficiently well (even C3, an occasional substitute for PS, C1 and C2). The task that we designed was difficult as images were presented individually, and required matching of each face to one of the 27 names (i.e., probability for correct responses was 1/27). PS performed very well with the original pictures, making only a few mistakes. However, she was much slower than normal controls, including C3, who was not highly familiar with the individuals displayed.

Controls' performance was not affected by removal of color and external facial information (experiment 1b). However, since controls' performance was at ceiling, the task was probably too easy for them, and this should certainly not be taken as evidence that color and external features do not contribute to personally familiar face recognition. In contrast, PS's performance dramatically deteriorated when she had to identify the same individuals based on grayscale images devoid of external features. This drop in performance emphasizes her prosopagnosia: she saw these children's faces for tens of hours every week during the 8-9 month term and was able to recognize them in the context of the kindergarten, provided that all cues were available. Apparently, however, PS relied on cues not necessary for healthy controls (at least not here), as her performance dramatically declined when these cues were unavailable. These results are in line with previous observations demonstrating that, when given

time, while prosopagnosics are sometimes still able to identify faces with external details, their performance drops when these external details are removed (e.g., Busigny et al., 2010b).

Overall, even with these cropped grayscale faces, PS's score (46%) was much higher than chance level, and superior to e.g. her performance during famous face identification (Rossion et al., 2003). However, here PS was tested in conditions similar to the kindergarten: she was aware that a limited set of faces — all personally familiar — would be presented. This contrasts to a situation of uncertainty, when an unknown number of famous faces and unfamiliar faces are presented at random. Here PS was also aware that faces were only presented once or twice, and she could thus use this knowledge as a cue to better match faces with their names (*"I have already seen the picture of child X, so this one must be Y"*). In fact, her performance at unfamiliar/familiar decision tasks, i.e. in conditions of uncertainty with the same face set, is substantially worse (61% for upright familiarity decisions; Busigny & Rossion, 2010, Experiment 5; see also Figure 3). Nonetheless, her performance in the present experiments indicates that she is somehow able to use internal features to identify these familiar faces learned in a real life setting. This experiment therefore provided a platform to study the nature of the information that the patient preferentially uses for personally familiar face identification and recognition, as assessed in the subsequent experiments.

Experiment 2: Identification of Anti-Caricatures

Rationale

The previous experiment tested PS's ability to identify individuals with whom she was personally familiar (i.e., correctly select a name for assignment to a given face). In Experiment 2 we aimed to test whether the *quantity* of information available on the whole face, irrespective of specific subtypes of information (i.e., parts, color, spatial frequencies, etc.) determines PS's (and

controls') performance at familiar face identification. To this end, we designed an experiment in which we presented the faces of 16 female children (cropped, color), as well as corresponding faces containing progressively less identity-specific information. These were generated by morphing each original face with the average of the 16 faces, creating so-called anti-caricatures containing parametrically varying amounts of identity information (see below and Figure 2a). We anticipated that decreasing identity information would lead to a steeper decline in performance for PS as compared to controls.

Stimuli and Procedure

To generate the anti-caricature stimuli required for this experiment, we selected the maximum even number of children of the same gender. We thus used 16 *original* (cropped, colored; see Figure 2a, 100%) females' face stimuli as a basis for anti-caricature creation; a preparatory step necessitated creation of an average face, as described in the following. Using MORPHEUS PHOTO MORPHER v3.01 we created morph continua of pairs of faces. For each face, 200 points were placed on the critical features (encompassing the pupils, iris, eye bulb, eyelid, eyebrow, mouth, nose, nostril, the middle of forehead, the middle of chin, and the face outline; see also Ramon, Dricot & Rossion, 2010; Ramon & Van Belle, 2016) to allow smooth transitions between the stimuli. Per morph continuum we derived the morph stimuli containing 50% of each contributing identity; based on these 8 stimuli we again created pairs of faces to be morphed in the same fashion. This procedure (using the 50% morphs from the previous averaging procedure as extremes for the new morph continua to be created) was repeated until we obtained a single final *average face* (see Figure 2a), to which all of the 16 *original* (100%) faces contributed. Finally, we selected the 16 *original* faces to create the same number of morph continua, the extremes of which consisted of a given *original identity* and the *average face* in order to obtain anti-caricatures. From each morph continuum we selected

stimuli that represented an *original* face by 100-20%, with 20% increments. Thus, per identity we obtained five stimuli, which differed in terms of their resemblance with the average created from all 16 *original* faces. These 80 experimental stimuli (displayed on white background, subtending on average $13.1^\circ \times 10.9^\circ$ of VA) were presented individually (unlimited presentation duration) for subjects to identify verbally; consecutive trials were initiated by the experimenter upon response. Using E-prime 1.1 each stimulus was presented four times throughout the entire experiment, once per block (80 randomly presented trials per block), resulting in a total of 320 trials per participant.

Results

Controls performed at ceiling, except for the most difficult condition (20% difference, Figure 2b and Table 2). PS's accuracy scores were below those of normal controls' overall, and she showed a main effect of *morph level* ($\chi^2_4=59.06$, $p<.001$) due to a drop of performance at the 20% morph difference between faces.

Controls' RTs increased with decreasing amount of original face identity information (main effect of morph level, C1: $F_{4,295}=45.12$, $p<.001$; C2: $F_{4,299}=37.99$, $p<.001$); this was also the case for PS ($F_{4,208}=10.68$; $p<.001$). RTs were significantly elevated for PS (C1: $t_{1,7}=5.11$, $p<.01$; C2: $t_{1,7}=5.37$, $p<.01$), but the slope did not differ from controls' (C1: $t_{1,6}=.04$, ns ; C2: $t_{1,6}=.005$, ns).

Discussion

Compared to Experiment 1, PS's performance improved when she dealt with fewer children's faces (here: only those of 16 females), and hence was subject to less ambiguity. Additionally, all stimuli contained color information and moreover, the same 16 pictures were repeated. Nevertheless, her performance remained well below controls' levels, which were at ceiling for all conditions, except for rare misidentifications when the amount of identity information was the lowest (i.e., 20%). Relative to her performance in general, PS's performance was also lower in

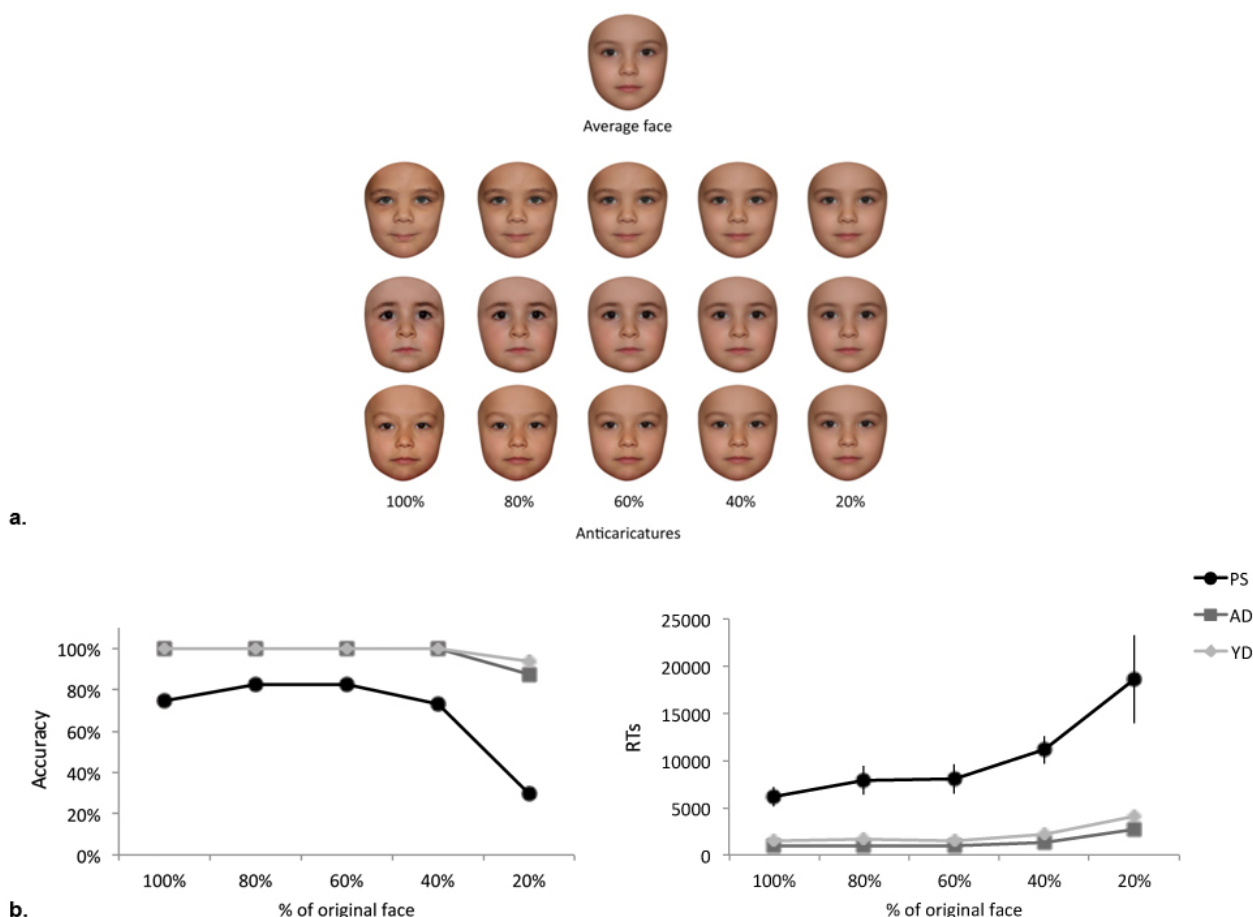


Figure 2. Stimuli and results for Experiment 2: Identification of Anti-Caricatures. **a.** Examples of stimuli created. Each row depicts an original (far left, 100%) face along with the anti-caricature stimuli created by morphing it (with 20% increments) with the above depicted average face (generated from all 16 originals; see Methods). **b.** Results of Experiment 2. Shown here are accuracy scores and correct RTs (with standard errors) for PS and her two age-matched controls.

that condition only, accompanied by a substantial increase in RTs of the same order of magnitude as the controls (i.e., 3 times slower than at 100%). Overall, the experiment probably lacked sensitivity for normal controls, since their performance was at ceiling. However, most importantly, PS's performance was stable between 100% and 40%, suggesting that it is not the *quantity* of identity-specific information present across the whole face that matters. Rather, this result suggests that PS is unable to use *specific* sources of information to recognize faces, even when this quantity of information is high (for the same pattern of profile on unfamiliar faces, see Busigny et al., 2010a). The next experiments therefore aimed at determining the nature of this information.

Experiment 3: “Bubbles” — Diagnosticity of Facial Information

Rationale

Here we aimed to assess the diagnosticity of different types of facial information for PS without a priori assumption about the nature of this information, using response classification with faces (Haig, 1985). Specifically, we used the “Bubbles” response classification method (Gosselin & Schyns, 2001). In our previous study using this approach (Caldara et al., 2005), PS and normal controls were required to learn grayscale pictures of unfamiliar faces, thereupon presented over thousands of trials through Bubbles masks, in order to identify the information diagnostic for face identification. Here, we designed an original 2AFC version of the Bubbles task with color photographs of faces learned in real-life.

Stimuli and Procedure

The same high-quality full-front color photographs of the 27 children described above were used (see Figure 1a). They were translated, rotated, and scaled to minimize the mean square of the difference between twenty landmark positions and the average of these landmark positions across all faces; and interocular distance was set to 100 pixels (approximately 2.35° of VA at a viewing distance of 35 cm). Stimuli were created by sampling the face images by presenting them behind an opaque mask punctured by randomly located Gaussian apertures having a standard deviation of 10 pixels or about 0.1° of VA (i.e., “bubble mask”). The number of bubbles was adjusted on a trial-by-trial basis using the QUEST algorithm (Watson & Pelli, 1983) to maintain a correct identification rate of approximately 75%. On each trial, stimuli were mirror-reversed with a probability of .5. The resulting images, exemplified in Figure 3, are sparsely sampled faces on a mid-gray background. PS completed 200 blocks of 108 trials (21 600 trials in total, over months of testing); C1 completed 20 blocks of 108 trials (2160 trials in total). On a given trial, two stimuli appeared side by side at the center of the computer monitor with the name of a child underneath (Times New Roman 28). The face images differed but they were partially revealed by the same bubble mask. Participants were instructed to place the mouse cursor on the stimulus partially revealing the face corresponding to this name and to click on the mouse button. The stimuli remained on the screen until a response was provided, upon which the next trial was initiated; no accuracy feedback was provided. The experiment was run on a MacBook Pro in the Matlab environment, using functions from the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997).

Results

Over the 20 blocks that she completed, C1 required an average of 8.43 bubbles ($SD=3.79$) to maintain performance at 75% correct and responded in 6.12s on average ($SD=1.64$). We

split the data of PS in ten independent segments of 20 successive blocks. On the first segment she required an average of 35.41 bubbles ($SD=19.57$) to maintain performance at 75% correct, and she responded in 6.31 s on average ($SD=1.24$). Overall, PS required an average of 19.89 bubbles ($SD=11.02$; range=[12.07:35.41]) to maintain performance at 75% correct, and she responded in 4.67 s on average ($SD=.59$; range=[4.10:6.31]).

To uncover which facial cues led more often to accurate identification, we performed a least-square multiple linear regressions between accuracies (predictive variable) and bubble masks (explanatory variable). The outcome of this regression is a 256 by 256 plane of regression coefficients which we call classification images (Eckstein & Ahumada, 2002; Gosselin & Schyns, 2004). We derived one such classification image for C1 and ten comparable ones with respect to the number of trials for PS (i.e., based on ten independent segments of 20 successive blocks). These classification images were smoothed with a Gaussian kernel having a standard deviation of 10 pixels and transformed into z-scores. Any significant positive local divergence from uniformity in our group classification images would indicate that the corresponding part of the stimuli led to more accurate responses. We conducted one-tailed Pixel tests (Chauvin et al., 2005) on the classification images ($S_r=43,691$; $Z_{crit}=3.75$; $p<.05$). The statistical threshold provided by this test corrects for multiple comparisons while taking the spatial correlation inherent to our technique into account. Results are shown in Figure 3; statistically significant areas are represented as colored blobs superimposed onto one of the base faces. Numbers above the classification images are ratios of the mean Z-scores in the eye and mouth areas, respectively. Thus, a ratio larger than 1 indicates greater use of the eyes than the mouth, while a ratio smaller than 1 indicates a greater use of the mouth than the eyes.

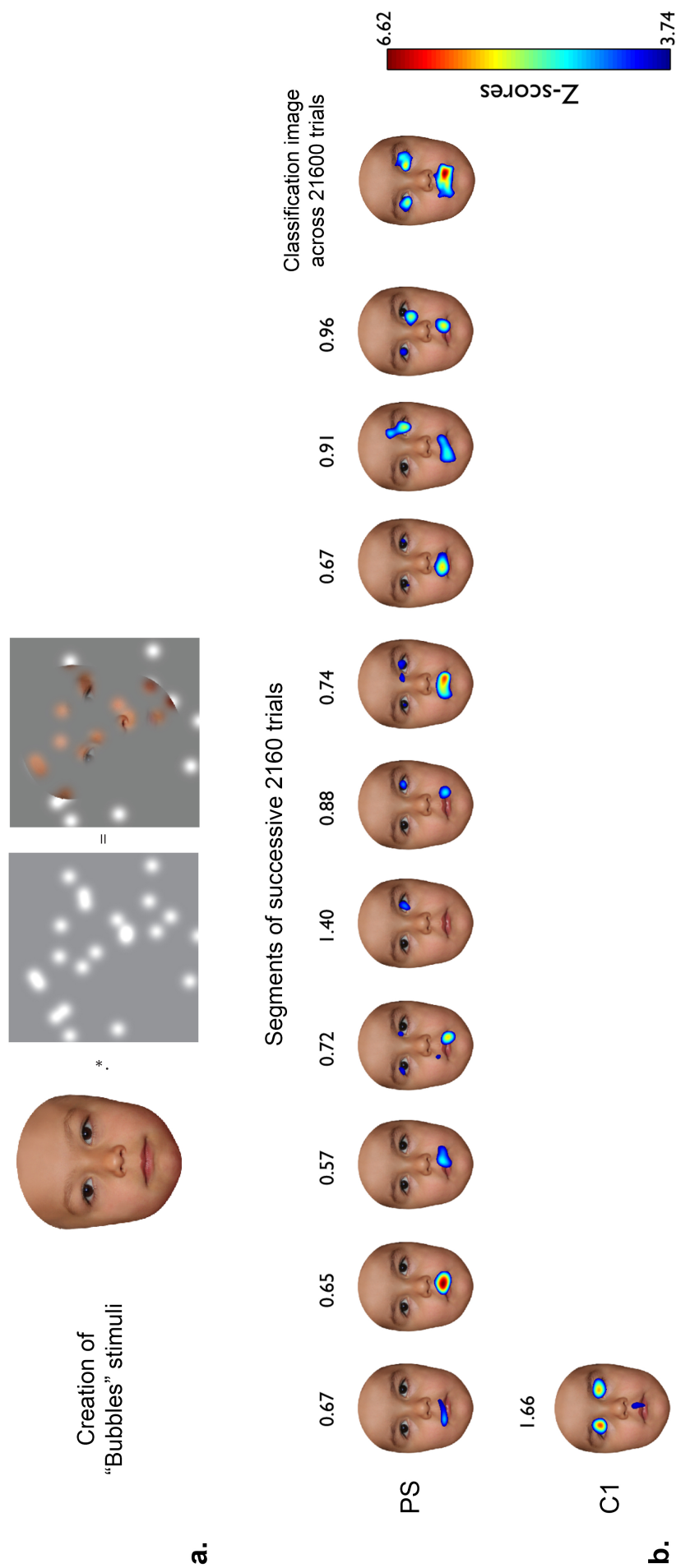


Figure 3. Stimuli and results for Experiment 3: “Bubbles.” — Diagnosticity of Facial Information. a, Stimuli were generated by overlaying an opaque mid-gray mask punctured by a number of randomly located Gaussian apertures on a face. b, Classification images for PS (derived from segments of 2160 successive trials and across all 21600 trials; from earliest to latest from left to right) and C1 (derived from 2160 trials). Statistically significant areas are represented as colored blobs superimposed onto one of the base faces ($p < .05$). The numbers above the classification images are ratios of the mean Z-scores in the eye and mouth area.

Discussion

The response classification images, obtained by comparing the sum of stimuli leading to correct identification to the sum of images associated with incorrect responses, revealed a striking difference between PS and the healthy participant (C1). While, in line with previous observations in normal observers (Gosselin & Schyns, 2001), the normal participant exhibited a dominant reliance on the eye over the mouth region, PS predominantly used information located on the mouth. Remarkably, despite the fact that she saw those particular cropped color faces 21,600 times, PS's strategy remained remarkably stable. Only one of the ten 2,160-trial segments led to a ratio greater than 1, albeit smaller than the ratio associated with the only 2,160-trial segments performed by the normal control. This is in line with Caldara et al.'s (2005) findings with grayscale images of unfamiliar faces. Note that compared to this previous study, PS also utilized information conveyed by the eye region here, albeit with some variability across sessions, suggesting changes in strategy while attempting to identify the faces. This relatively increased reliance in extracting diagnostic information from the eyes compared to the previous study (Caldara et al., 2005) may be due to the differences between artificially and naturally learned faces. Also, the presence of color information here, but not in the study of Caldara et al. (2005), may have increased the eyes' diagnosticity for face identification for PS (see also Jiang et al. (2011), who reported that PS relies relatively more on color and texture than shape information). Overall, these observations support the view that the representations of personally familiar faces are *qualitatively* altered in acquired prosopagnosia: PS does not merely require *more* information than a typical observer — she also relies on a *different kind* of information, preferentially using the mouth at the expense of the eye region.

Experiment 4: Recognition of Isolated Features

Rationale

Previous studies with PS have identified her increased reliance on the mouth region when attempting to recognize experimentally learned faces (Caldara et al., 2005), discriminate pictures of unfamiliar faces (Rossion et al., 2009; Ramon & Rossion, 2010) or identify familiarized faces presented through Bubbles masks (experiment 3), as well as personally familiar faces presented in full view during eye movement recordings (Orban de Xivry et al., 2008), or through gaze-contingent displays (Van Belle et al., 2010b). Other studies that have supported this increased reliance on the mouth have used individual face discrimination tasks (Bukach et al., 2006; 2008; Barton, 2008b; Busigny et al., 2010a; Pancaroglou et al., 2016). Here, in order to provide further support for these findings, we sought to assess PS's ability to identify personally familiar faces based on isolated facial features, i.e., eyes or mouth only, and contrast her performance with normal controls'. We expected PS to show better performance on mouth than eyes trials, while the opposite was expected for controls. In Experiment 4a (verbal identification) we anticipated relatively low performance for PS, and therefore used a 2AFC name assignment task in Experiment 4b with the aim of obtaining higher accuracy scores. Across changes in tasks we sought to increase the likelihood of finding dissociable performance across conditions for both behavioral measures for PS, albeit anticipating potential ceiling effects for controls.

Stimuli and Procedure

Photographs of the 27 kindergarten children described above were processed in a manner to create two different types of stimuli containing isolated facial features—either the eyes (without eyebrows) or the mouth. The resulting colored stimuli (see Figure 4a) encompassed a 230x40 and 130x40 pixels area for eyes and mouths, respectively, corresponding to 4.5°x.8° and 2.5°x.8° of VA.

Experiment 4a: Verbal identification of isolated facial features. For Experiment 4a the (initially randomized) stimuli were presented in isolation in the same sequential order to all subjects in the course of a verbal identification task. Each stimulus was presented for unlimited viewing duration until subjects provided a name (responses were recorded by the investigators in written form) and subsequently pressed the space bar to initiate presentation of the next stimulus. Trials were separated by a 1000ms inter-trial-interval (ISI) accompanied by a blank (white) screen. Thus, there were two conditions (feature type) with 27 trials each, resulting in a total of 54 trials.

Experiment 4b: Forced-choice recognition of facial features—name assignment. In Experiment 4b subjects completed a 2AFC matching task, during which isolated features (identical to those used for Experiment 4a) were presented in pairs, with a child's name presented above. One of the probes corresponded to the name, the other one was a distractor. With exception of C2, all subjects performed the task with eyes first. As each feature was paired with two possible distractors, participants completed 54 trials per feature type (en bloc, separated by a pause after 27 trials). All participants were presented the same pairs; order was randomized across subjects. Participants were required to identify the target item as correctly and rapidly as possible by pressing a left or right key. Consecutive trials, initiated upon response, were separated by a 1000ms ISI. The left and right positions of the target stimuli were counterbalanced across test items; feedback was not provided. Prior to each block, subjects completed four practice trials excluded from analyses.

Results

Experiment 4a: Verbal identification of isolated facial features. Participants' performance across conditions is displayed in Figure 4b and reported in Table 3a. In terms of accuracy, C3 showed a significant advantage for identification based on eyes as compared to mouths ($\chi^2_1=7.94$, $p<.01$); the other controls

showed a non-significant trend in the same direction (C1: $\chi^2_1=2.86$, ns ; C2: $\chi^2_1=1.48$, ns). All controls required significantly more time to identify the mouths than the eyes of children (C1: $t_{31}=2.57$, $p<.01$; C2: $t_{44}=1.70$, $p<.05$; C3: $t_{31}=2.91$, $p<.005$).

PS, on the other hand, displayed a distinctly opposite pattern: she was much better at identifying children based on the isolated mouth as compared to the eyes ($\chi^2_1=8.33$, $p<.01$), without any difference in RTs between conditions ($t_{16}=.09$, ns). Furthermore, regarding identification of mouths, PS's accuracy score did not differ from controls ($t=.30$, ns) despite exhibiting significantly prolonged RTs ($t=9.66$, $p=.005$). Contrariwise, she was significantly worse than controls at identification based on the eyes ($t=6.54$, $p=.01$), and significantly slower ($t=22.00$, $p=.001$). Naturally, the benefit for mouths over eyes displayed by PS is small (~400ms) in light of her generally prolonged RTs. Therefore, to account for overall differences in RTs, per subject we calculated RT-indices by dividing the average RT per condition by the sum across both conditions. These indices reflect the relative advantage of identification under the experimental conditions. Analyses of RT indices using Crawford and Garthwaite's (2005) RSDT indicate that the difference between the two conditions is significantly different from that observed in controls ($t_2=2.94$, $p<.05$). As evident from Figure 5b, compared to controls, PS's RT index for eyes was larger, whereas her RT index for mouths was lower.

Experiment 4b: Forced-choice recognition of facial features—name assignment. Results are displayed in Figure 4c and reported in Table 3b. Controls performed at ceiling for eyes trials. C1 made significantly more mistakes for mouth trials ($\chi^2_1=4.15$, $p<.05$), while C2 and C3's accuracy scores did not differ across the two conditions ($\chi^2_1=1.01$, ns). They were also all faster for eyes as compared to mouth trials (C1: $t_{98}=2.24$, $p=.01$; C2: $t_{102}=2.29$, $p=.01$), although this difference did not reach significance in C3 ($t_{102}=.72$, ns).

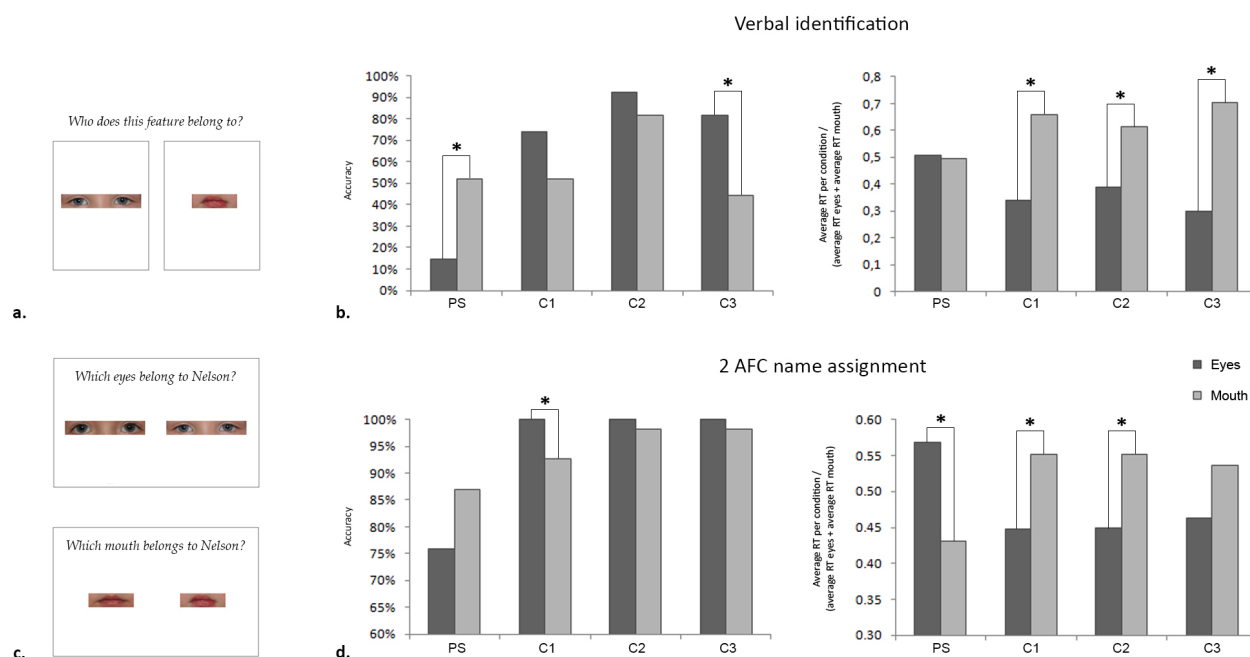


Figure 4. Stimuli and results for Experiment 4: Recognition of Isolated Features. a, Examples of stimuli (individual facial features) shown on each trial and b, subjects' performance (accuracy and RT-indices) in Experiment 5a (verbal identification). c, Examples of trials which involved presentation of feature pairs and d., subjects' performance (accuracy and RT-indices) in Experiment 5b (2AFC name assignment).

PS, on the other hand, displayed a non-significant trend for better performance when recognizing mouths as compared to eyes ($\chi^2_1=2.21$, *ns*) and was significantly faster for mouth as compared to eyes trials ($p<0.01$), despite being much slower than controls irrespective of feature type (eyes: $t=12.51$, $p<0.005$; mouth: $t=6.74$, $p=.01$). Crawford and Garthwaite's (2005) RSDT confirmed that the condition-dependent difference in PS's RTs differed significantly from that observed for controls ($t_2=6.98$, $p<0.01$). This is reflected in individuals' indices (see Figure 4c): PS's index for eyes was higher than that of controls, whereas her index for mouths was lower.

Discussion

Experiments 4a and 4b show that typical observers perform better at recognizing familiar identities based on the eye region compared to the mouth, while PS shows the exact opposite pattern. Her accuracy scores for the eyes alone were extremely low (4/27 children identified in Experiment 4a), while her accuracy score for the mouth was within the normal range. This experiment indicates that PS's increased reliance on the mouth region, relative to typical observers, is not only

due to the nature of the unfamiliar face stimuli used in previous studies, or to the specific tasks used—she seems to have a long term representation of the faces that privileges the mouth at the expense of the eye region.

In our previous work, we have associated this lack of usage of the eye region to the loss of holistic face processing: this region of the face, which is made of a multiple elements, is highly diagnostic for an observer who is able to process these elements as an integrated unit. However, for an observer such as PS who is no longer able to process an individual face as an integrated unit, the eye region may have lost its diagnosticity. This is because PS would have to process each of the features composing this eye region in isolation, making this process particularly time-consuming (Rossion, 2008; 2013).

To support this view, it is important to show that PS does not process familiar faces holistically, or at least as holistically as typical observers. A single previous experiment supports this view: contrary to the same control participants as tested in the present paper (C1, C2), PS showed no inversion effect in a 2AFC forced-choice familiarity decision involving

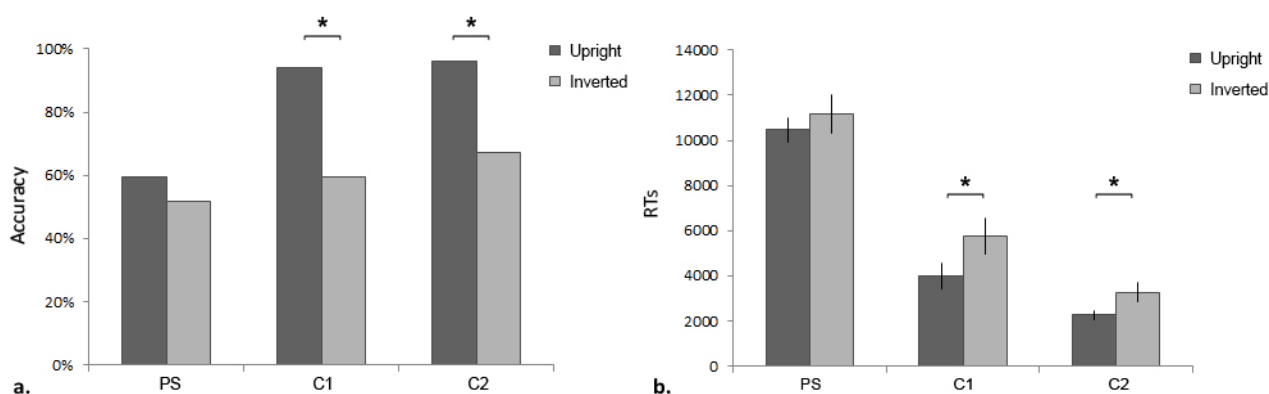


Figure 5. Results of PS and two control participants in a familiarity decision task with upright and inverted faces. The data displayed here were originally reported by Busigny & Rossion (2010; experiment 5). Contrary to PS, whose performance did not vary with stimulus orientation, C1 and C2 exhibited a strong FIE, both in terms of a, accuracy scores and b, correct RTs.

unfamiliar faces and the same children used here (Experiment 5 of Busigny & Rossion, 2010; see Figure 5). In the remaining experiments of this paper we further investigate holistic processing of personally familiar faces to more firmly establish the presence of PS' s deficient holistic processing of familiar faces.

Experiment 5: Composite Face Effect

Rationale

Experiment 5 aimed at testing PS with the most commonly used paradigm to probe holistic face processing: the composite face paradigm (for reviews see Rossion, 2013; Murphy et al., 2016). In their seminal report of the composite face effect, Young and colleagues (1987) used pictures of famous faces. In their experiment, the top half of Marilyn Monroe was for instance paired with the bottom half of Maggie Thatcher, with subjects required to identify each of the two halves. The basic finding was that identification of the face halves was much more difficult when they were spatially aligned with each other, forming a whole new configuration, compared to when they were misaligned. Subsequently, Hole (1994) adapted the paradigm with unfamiliar faces, showing that matching two identical top halves of a face is difficult if they are aligned with different bottom halves. The overwhelming majority of studies have used the paradigm with unfamiliar faces (Rossion, 2013). Here, we designed a task in which we asked PS and her two

colleagues to verbally identify each child's face top half, when it was aligned or misaligned with the bottom half of another identity. We replicated Young et al.'s (1987) original finding with personally familiar faces for each of the normal participants. However, PS's performance in top part face identification was so low that the absence of composite effect for the patient could not be clearly interpreted. To address this issue, in keeping with the above described procedure for obtaining sufficiently high accuracy scores, we designed two additional tasks (5b and 5c) involving 2 AFC forced-choice name assignment and familiarity decisions.

Stimuli and Procedure

Experiment 5a: Verbal identification of composite faces. Composite stimuli consisting of top and bottom halves of two different children faces were created using Adobe Photoshop. The original photographs were cropped of hair and external features, and were gray-scaled in order to maximize the magnitude of the composite effect (Retter & Rossion, 2015). The resulting faces (740x870 to 830x960 pixels) were fitted onto a white background, and were then separated by inserting a .6mm gap located 30 pixels above the upper nostril limit to clearly identify the top part (Rossion & Retter, 2015). The 25 faces most concordant regarding completion were used to create the composite stimuli. This was done by combining a top part with the lower parts of two randomly chosen (same sex)

children. The bottom parts were at times slightly modified to fit the boundaries of the nose or face contour. These faces constituted the *aligned face set*. To create misaligned faces, the lower parts of the faces were then laterally offset to the right side by approximately a third of the face width, which is largely sufficient to disrupt the composite face effect (Laguesse & Rossion, 2013). Both sets were then reduced in size by 75%. The resulting stimuli (see Figure 6a) were approximately 260 pixels high (5° of VA), and 210–225 pixels (aligned; $4.1\text{--}4.4^\circ$ of VA) or 250–265 pixels (misaligned; $4.9\text{--}5.2^\circ$ of VA) wide. The 100 stimuli (50 per condition) were randomly presented across two experimental blocks of equal length (same across subjects). All subjects were tested on a laptop located 60cm in front of them (17 inch, 60Hz refresh rate; 1024x768 pixel resolution). Stimulus presentation was controlled using E-prime 1.1. A stimulus was presented against a white background until subjects provided a name (responses recorded by the investigators in written form) and pressed the space bar to initiate presentation of the next stimulus. Consecutive trials were separated by a 1000ms ISI accompanied by a blank (white) screen.

Experiment 5b: Forced-choice recognition of composite faces—name assignments. The same stimuli and experimental setting as described for Experiment 5a were used in Experiment 5b. The only differences lay in the task, and thus the design. While subjects were again instructed to perform decisions based on top parts of composite faces, here each experimental trial consisted of presentation of two composite face stimuli, side-by-side, that were both either aligned, or misaligned. Each face pair appeared with a name located above the pair (capital letters encompassing 245–690 pixels in width and 80 pixels in height depending on the name). Participants performed a forced-choice recognition task, deciding which top corresponded to the name provided above (see Figure 6a). Importantly, the task-irrelevant bottom face halves of both stimuli presented within a trial were identical.

The 50 misaligned and aligned face pairs appeared twice each, with the name corresponding to either the right, or left composite face part. The experiment comprised 200 randomly experimental trials separated into 4 blocks of equal length. For half of the aligned and misaligned trials the correct face stimulus was located on the left. Subjects were instructed to attend to the top half and indicate, as accurately and rapidly as possible, which of the two corresponded to the above-located name by button press.

Experiment 5c: Forced-choice recognition of composite faces—familiarity decisions. For Experiment 5c new composite faces were created in the same manner described above. They differed from the previous ones in that they involved combinations of familiar and unfamiliar halves, which were presented horizontally aligned or misaligned. As before, an individual composite stimulus was presented for unlimited viewing duration. Here, however, subjects were required to perform forced-choice familiarity decisions of top parts (see Figure 6c). The respective task-irrelevant bottoms were always parts of the face of a familiar child. Thus, the composite face stimuli presented here were created from unfamiliar or familiar tops, paired with familiar face bottoms. The unfamiliar tops were taken from photographs of children of the same age group who attended a kindergarten in Germany. Stimuli consisting of both familiar face top and bottoms were taken from the aforementioned experiments (half of the stimuli used for 5a, and 5b; each part combined with a respective other of one, as opposed to two parts of a different face). This resulted in a total of 50 familiar-face-only composite stimuli (25 mis-/aligned), and 50 containing parts of familiar and unfamiliar faces. Participants were instructed to indicate whether top parts belonged to a personally familiar child by pressing one of two keys; upon response the next trial was initiated (no feedback provided). The experiment incorporated 200 trials randomly assigned to one of four blocks of equal length, within which the trials were

presented in the same order to all of the subjects. Only “familiar” trials were included in the analysis, the remaining ones served as catch trials (not analyzed).

Results

Experiment 5a: Verbal identification of composite faces. PS’s accuracy rate was extremely low—overall she recognized only 11% of the composite face tops, while all controls scored at about 90%; additionally, and as before, she was much slower than controls (see Table 4a). Controls showed higher accuracy scores for misaligned as compared to aligned composite stimuli; this difference was significant for C2 only ($\chi^2_1=7.11$, $p<.01$; C1: $\chi^2_1=1.78$, ns). However, RTs were significantly longer for aligned as compared to misaligned trials for both controls (i.e., a CFE; C1:

$t_{77}=3.12$, $p=.001$; C2: $t_{85}=2.96$, $p<.005$). PS’s accuracy and RTs did not differ in the aligned and the misaligned conditions ($\chi^2_1=.92$, ns ; $t_9=.46$, ns). Thus, only controls benefitted from top and bottom part misalignment, but PS’s performance was too slow to draw clear conclusions.

Experiment 5b: Recognition of composite faces—forced-choice name assignment. PS’s overall accuracy was still lower than controls’ (who were at/near ceiling across conditions), but her performance was markedly better (~70%) than when verbal identification was required (experiment 5a; compare Table 4a and Table 4b). With respect to RTs, PS was also still slower than both controls, although the difference was less pronounced than in the previous experiment. Controls’ accuracy did

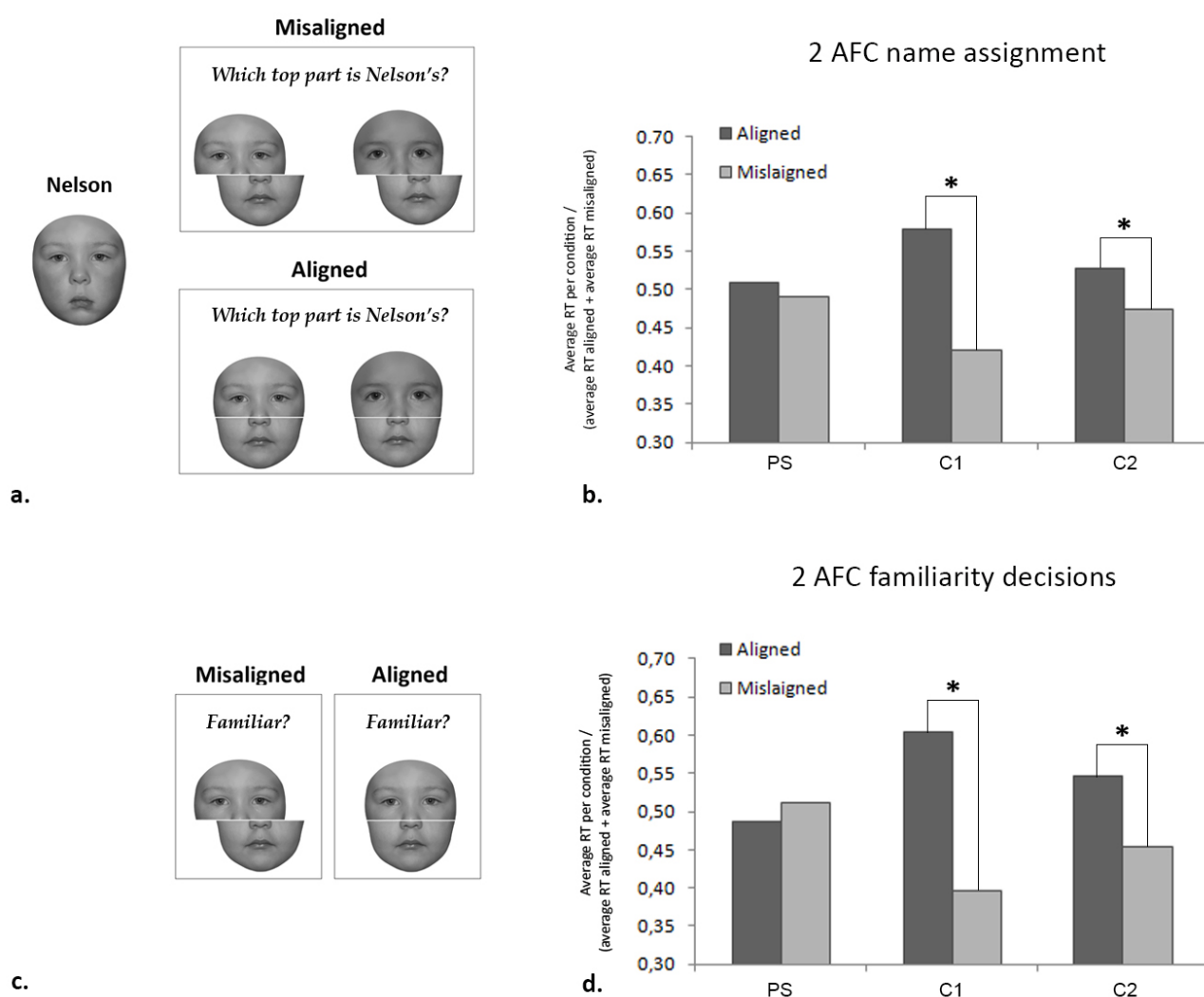


Figure 6. Stimuli and results for Experiment 5: Composite Face Effect. **a**, Examples of stimuli created from an original face (left; name changed) and **b**, subjects’ RT indices for Experiment 5b (higher values indicate worse performance). **c**, Examples of stimuli presented and **d**, subjects’ RT indices for Experiment 5c. Asterisks indicate significant differences between conditions for individual subjects’ RTs.

not differ across conditions (C1: $\chi^2_1=1.02$, *ns*; C2: $\chi^2_1=1.85$, *ns*), but they were significantly faster for misaligned than aligned trials (C1: $t_{188}=4.43$, $p<.0001$; C2: $t_{189}=2.95$, $p<.005$). PS's performance did not vary as a function of alignment, neither for accuracy scores ($\chi^2_1=.21$, *ns*), nor RTs ($t_{133}=.41$, *ns*). These differences between PS and controls are reflected in RT indices (see Figure 6b): only controls' RTs decreased due to misalignment of top and bottom parts.

Experiment 5c: Recognition of composite faces—forced-choice familiarity decisions. The results of the present experiment are reported in Table 4c and displayed in Figure 6d. Overall, PS scored well above chance (73%, $p<.0001$). She was faster than in experiments 5a and 5b, albeit still slower than controls. C1 was significantly more accurate for misaligned trials ($\chi^2_1=7.11$, $p<.01$); C2 was at ceiling for both conditions. However, both controls were significantly slower at performing familiarity judgments based on top face halves when these were aligned with bottom face halves (C1: $t_{86}=4.01$, $p<.0001$; C2: $t_{95}=3.04$, $p<.005$). PS's results were entirely different than those of her controls. She obtained significantly higher accuracy scores for aligned trials ($\chi^2_1=4.11$, $p<.05$), while her RTs did not vary as a function of alignment ($t_{70}=.48$, *ns*). The RT indices of all participants (see Figure 6b) highlight the benefit for misaligned face halves for controls, but its absence for PS.

Discussion

Typical participants performed better and/or faster at verbal identification of top parts of composite faces when these top halves were misaligned rather than aligned with bottom face halves, i.e., showed a composite effect. This replicates Young et al.'s (1987) original composite face effect, at least in correct RTs, with large effects observed here for each of the two control participants. PS showed no such difference between the conditions. However, her performance was too low to be fairly evaluated. The altered task requirements (i.e., from verbal identification to 2AFC name assignment) led to a substantial increase in

PS's performance. However, even in these conditions, PS's performance remained unaffected by spatial alignment. This absence of a beneficial effect of misalignment of top and bottom parts further supports the previous findings indicating an absence of holistic processing for the prosopagnosic patient PS (Ramon et al., 2010; Van Belle et al., 2010a; Busigny & Rossion, 2010). Importantly, control participants, despite being at ceiling for accuracy, showed a composite effect in terms of correct RTs. When familiarity decisions of top parts of composite faces were required, controls again exhibited a composite effect. However, despite acceptable performance, PS did not show this pattern of results, and even achieved a significantly higher accuracy score when top and bottom composite face parts were aligned. Thus, overall, these experiments replicate previous reports of a lack of composite face effect for PS with unfamiliar faces (Ramon et al., 2010), pointing to a loss of holistic processing. That is, rather than involuntarily integrating the two halves of a familiar face composite stimulus together into a new configuration as do controls, PS appears to process the top and bottom halves of faces independently of each other.

Experiment 6: Whole-Part Advantage

Rationale

To strengthen the findings of experiment 5, we probed PS's ability to recognize personally familiar individuals based on facial information using another well-established measure of integration: the whole-part advantage paradigm (Davidoff & Donnelly, 1990; Tanaka & Farah, 1993; reviewed by Tanaka & Simonyi, 2016), which, to our knowledge, has not been previously tested with personally familiar faces. In this paradigm, participants are usually presented with pairs of stimuli: either two isolated parts (two pairs of eyes for instance) or two whole face stimuli that differ according to that part only (two faces with different eyes). They are asked to determine which of the two corresponds to a target face presented shortly before. Usually, if

the facial configuration facilitates recognition of single parts, participants perform better for *wholes*, as compared to *parts* trials. In a previous study, PS did not show a whole-part advantage compared to a population of normal controls (Ramon et al., 2010). However, in typical participants, the whole-part face effect is usually weaker than the composite face effect, and it is not found in every control (e.g., Avidan et al., 2011; Ramon et al., 2010; Michel et al., 2006). Here, given the nature of the study, we had only two controls available, but the nature of the stimuli allowed us to build highly sensitive experiments to test effects of the experimental manipulations in each of our participants.

Stimuli and Procedure

Stimuli were created using the same 27 familiar and 9 unfamiliar children's faces used to create the stimuli for Experiment 5c. Unfamiliar, rather than familiar distractor features were used in this experiment because pilot testing showed that the use of familiar face distractors led to confusion (as subjects tried to recognize the familiar information of two faces combined in the foil stimulus). Here, each unfamiliar face was associated with three familiar faces of the same sex. For eye trials, to create a distractor stimulus for each familiar face, the eyes of three familiar face stimuli were swapped with those of an unfamiliar one using Adobe Photoshop. For mouth trials, the same procedure was applied. This led to a total of 81 stimuli: 27 original, "eye-distractors" and "mouth-distractors", respectively.

Experiment 6a: Whole-part advantage—forced-choice name assignment. In Experiment 6a, subjects completed a 2AFC matching task, in which they were either presented pairs of whole faces, or isolated features, with a child's first name presented above. One of the items of the pair corresponded to the child's name, and the other one was a distractor (see Figure 7a). Each stimulus was paired with one distractor; pairs presented were identical for all subjects (order randomized across subjects). Participants were required to identify the target item in the pair as accurately and rapidly as

possible by button press. The stimulus pair remained on the screen until subjects responded; consecutive trials were separated by a 1000ms ISI. Two blocks of 54 trials were presented; prior to the experiment subjects completed 4 practice trials excluded from analysis. The left and right positions of the target stimuli were counterbalanced across test items; participants received no feedback.

Experiment 6b: Whole-part advantage—forced-choice familiarity decisions. With the exception that no name was presented above stimulus pairs, experiments 6a and 6b involved the identical procedure and stimuli (see Figure 7a). In Experiment 6b subjects performed 2AFC familiarity decisions, in which they were required to indicate the side on which familiar eyes or mouths were presented (as parts or wholes). Thus, the task was more difficult than was the case for the previous experiment, as the search could not be constrained by the name, and the correct feature could belong to one of the 27 familiar faces. Our aim was to avoid controls performing at ceiling as was the case in some of the other experiments, and thus enable observation of a whole-part advantage in terms of accuracy scores as well. Naturally, the increase in task difficulty was associated with the risk of a dramatic decrease in PS's performance.

Results

Experiment 6a: Whole-part advantage—forced-choice name assignment. The results for experiment 6a are illustrated in Figure 7b and reported in Table 5a, separately for matching of eyes and mouths. Controls performed at ceiling for both the wholes and parts condition, for eyes and mouths. PS performed at about 80% with no difference between conditions ($\chi^2_1 = 0.06$, *ns*). Compared to each control, her performance was significantly less accurate and slower for every condition ($ps < .001$).

Concerning RTs, each control responded faster on *wholes* as compared to *parts* trials, both for eyes (C1: $t_{96} = 2.48$, $p < .01$; C2: $t_{103} = 2.29$, $p = .01$) and mouths (C1: $t_{99} = 3.40$, $p < .001$; C2: $t_{104} = 3.30$, $p < .001$). Contrariwise, PS's responses were faster for parts as

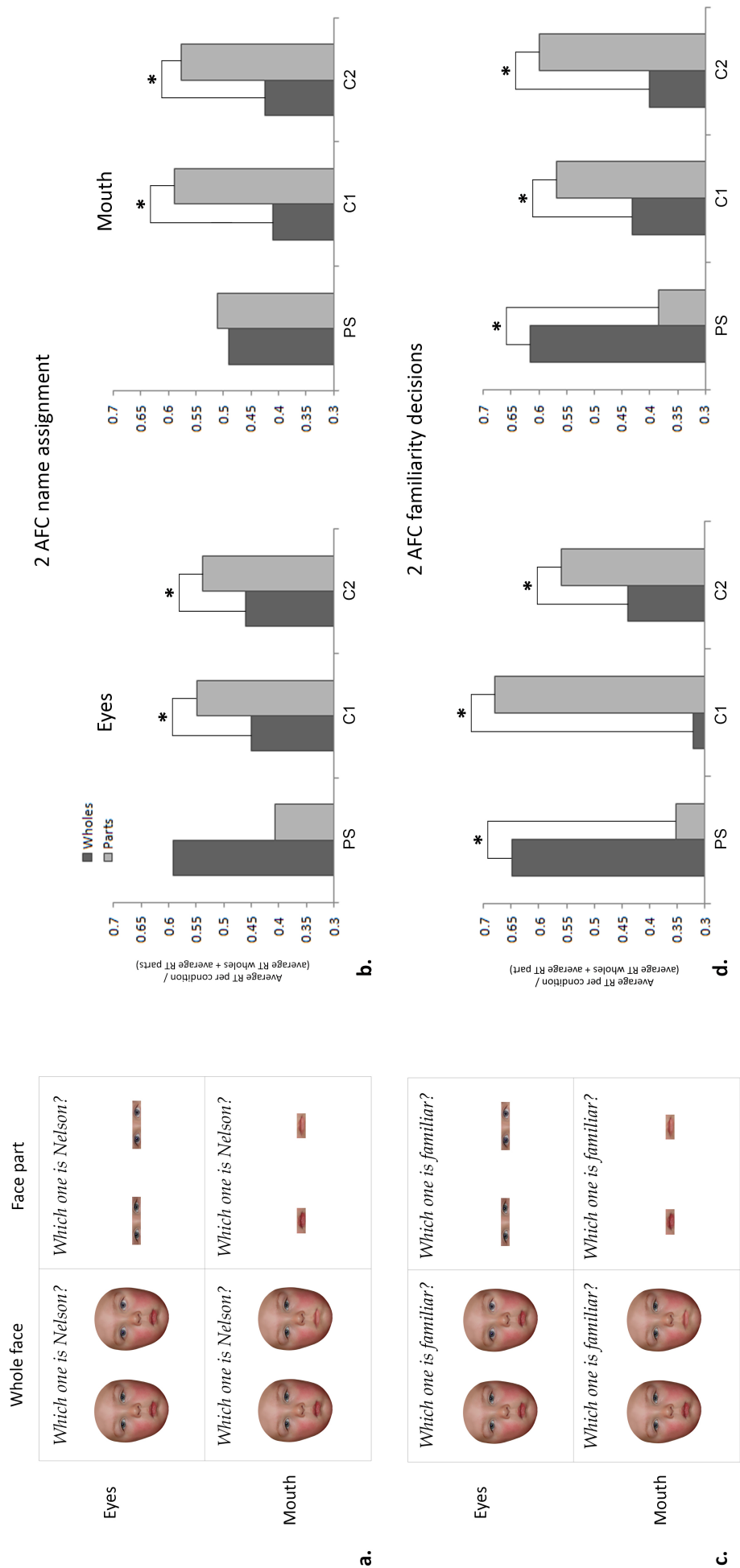


Figure 7. Stimuli and results for Experiment 6: Whole-Part Advantage. a, Examples of trials and b, subjects' RT indices during 2 alternative forced-choice (2AFC) name assignment (Experiment 6a). As depicted in c, the same trials are presented when subjects were required to perform forced-choice familiarity decisions (Experiment 6b); d, shows subjects' behavior for this task. In both experiments, task-relevant features were eyes or mouths (top and bottom rows in a. and c.); higher values in b. and d. indicate worse performance, asterisks indicate significant differences between conditions in terms of RTs.

compared to wholes for eyes ($t_{86}=2.70$, $p<.005$) while there was no difference in RTs for parts and wholes when the diagnostic feature was the mouth ($t_{81}=.34$, ns). The RT indices calculated per subject and condition under name assignment to eyes and mouths separately (see Figure 7b) illustrate the striking difference in RT profiles between subjects. Controls were generally faster if the features were embedded in the facial context (RTs *wholes* < RTs *parts*). For PS, however, whole face stimuli were associated with longer RTs if eye region was the task-relevant feature; for mouths RTs did not vary depending on the presence or absence of the facial context.

Experiment 6b: Whole-part advantage—forced-choice familiarity decisions. The results of experiment 6b are provided in Table 5b and illustrated in Figure 7c. Here C1 showed a whole-part advantage in terms of accuracy rates both for decisions based on eyes ($\chi^2_1=8.64$, $p<.01$) and mouths ($\chi^2_1=7.34$, $p<.01$). C2 made more mistakes under the parts condition ($\chi^2_1=4.15$, $p<.05$) but her performance was almost at ceiling. Irrespective of the nature of the part, PS's accuracy scores did not vary as a function of condition (i.e., performance for wholes did not differ from parts; eyes: $\chi^2_1=.65$, ns ; mouth: $\chi^2_1=3.65$, $p=.06$, *non-significant trend for whole > parts*). As in Experiment 6a, in comparison to both normal controls for each condition her performance was significantly lower ($ps<.0005$) and slower ($ps<.001$).

As in the previous experiment, the observations made for correct RTs were most informative. Each control responded faster on *wholes*, as compared to *parts* trials, both for eyes (C1: $t_{96}=4.47$, $p<.0001$; C2: $t_{100}=1.97$, $p<.05$) and mouths (C1: $t_{87}=2.13$, $p<.05$; C2: $t_{101}=4.83$, $p<.0001$). PS, on the other hand, was generally much slower under the *wholes* as compared to the *parts* condition (eyes: $t_{68}=4.97$, $p<.0001$; mouths: $t_{82}=3.92$, $p<.0001$). Thus, her superior performance on *wholes* as compared to parts trials for decisions based on mouths emerged at the expense of dramatically increased RTs (i.e., a speed-accuracy trade-off).

The RT indices calculated for each subject are displayed in Figure 7c. These demonstrate the benefit for wholes over parts trials displayed by controls, and the opposite pattern of performance observed for PS.

Discussion

In Experiment 6a, both controls exhibited a clear whole-part advantage in terms of correct RTs. PS's performance was in stark contrast to that of the controls: her performance was not influenced by the experimental manipulations, thus indicating the absence of a benefit for wholes over parts. In fact, PS was even slower for wholes than parts. In Experiment 6b, all participants performed better for wholes than parts, whereas PS showed no such difference. Most importantly, contrary to normal participants, who responded much faster to wholes than parts, PS's response times were particularly prolonged in the whole face condition. Hence, it seems that rather than benefitting from the presence of a whole face, it actually led to an increase in RTs for PS. Given that her performance was slightly better for the whole face condition, this slowing down for whole faces should not be over-interpreted, but rather interpreted as a trade-off. Therefore, again PS showed no whole-part advantage, as observed for both normal controls. Moreover, it is worth noting that again PS performed better and faster when having to discriminate the two faces based on the mouth than the eyes, irrespective of whether these parts were presented in isolation or embedded in whole faces.

Experiment 7: Representation of Overall Facial Geometry

Rationale

This experiment was designed to provide further support for the holistic processing impairment hypothesis, using an original paradigm developed by Barton et al. (2003). In this study, the authors manipulated the metric distances between the eyes and mouth of faces, moving the eyes closer together or further apart, while simultaneously moving the mouth up or down. In an oddity paradigm, the authors

found that combinations that more severely distorted the original triangular relation of the mouth and eyes (e.g., eyes closer and mouth down) were detected more efficiently than less distorting combinations that better preserved the original aspect ratio of the face (e.g., eyes farther and mouth down). This "geometric context effect" is interesting because it does not rely merely on the ability to evaluate metric distances between facial features (e.g., inter-ocular distance), something that PS can do if she is instructed about the nature (i.e., location) of the cue (Ramon & Rossion, 2010). Rather, one has to assess the *ratio* of the horizontal distance between the two eyes and the vertical distance between the eyes and mouth, thus having to consider the whole face configuration. Hence, this effect has been found for upright, but not inverted faces in normal participants, and it was absent in a case of acquired prosopagnosia, implying that this patient did not perceive faces holistically (Barton et al., 2003). To our knowledge, this effect, which was demonstrated for unfamiliar faces, has not been exploited in the literature (but see Ramon (2015a) for a recent report with personally familiar faces). Here, we designed an experiment in order to investigate participants' ability to appreciate the overall configuration of faces, in terms of the relative position of the constituent facial features. To this end, for all children's faces we created more and less distorting versions. We reasoned that efficient processing of facial configurations would lead to superior detection of alterations of original face configuration as opposed to their relative preservation. That is, for normal participants, but not for PS, "more distorted" faces were expected to be more easily rejected as foils than "less distorted" ones when presented together with the veridical version (Ramon, 2015a).

Stimuli and Procedure

Stimuli were created based on the color photographs of the 27 familiar faces used for the previous experiments. Images subtended a size of ~300x360 pixels at 72dpi. For each face stimulus four slightly distorted versions were

created by elevating or lowering the mouth (by 6 pixels, 1/60 of the face height), and increasing or decreasing the inter-ocular distance (by 10 pixels, 1/30 of the width of the face). The face stimuli subtended ~8x10.5° of VA, so that the differences between original and distorted faces corresponded to .27° of VA for the eyes, and .175° of VA for the mouth. Two types of changes were considered as "less distorting": increased inter-ocular distance accompanied by lowering of the mouth's position, and decreased inter-ocular distance accompanied by elevations of the mouth (both preserving the original facial configuration). Conversely, the other two modifications (eyes out, mouth up; eyes in, mouth down) were considered as "more distorting" (both altering facial configuration; see Figure 8a). Subjects completed a 2AFC task, which required veracity decisions between two versions of an individual's face (name provided above). Each trial consisted of presentation of an original face paired with one of its distorted versions (i.e., distractor); order of conditions was fully randomized. Participants were told that original faces would be paired with foils, but were not informed about the type of manipulations applied. They were required to indicate the location of the original face as accurately and rapidly as possible by pressing a corresponding key. Upon response the following trial was presented after a 1000ms ISI. After three practice trials (excluded from analyses) subjects completed two blocks of 54 trials each. The position of the target stimuli was counterbalanced across test items; no feedback was provided. Trials with RTs > 3SD of the mean RT per condition were excluded from analyses.

Results

Results are provided in Table 6 and illustrated in Figure 8b. While all controls, including C3 who was less familiar with the faces, performed above 90% independent of type of distortion, PS found this task extremely difficult. However, her overall performance was above chance level (63%; $p < .05$), albeit much lower than the controls considered

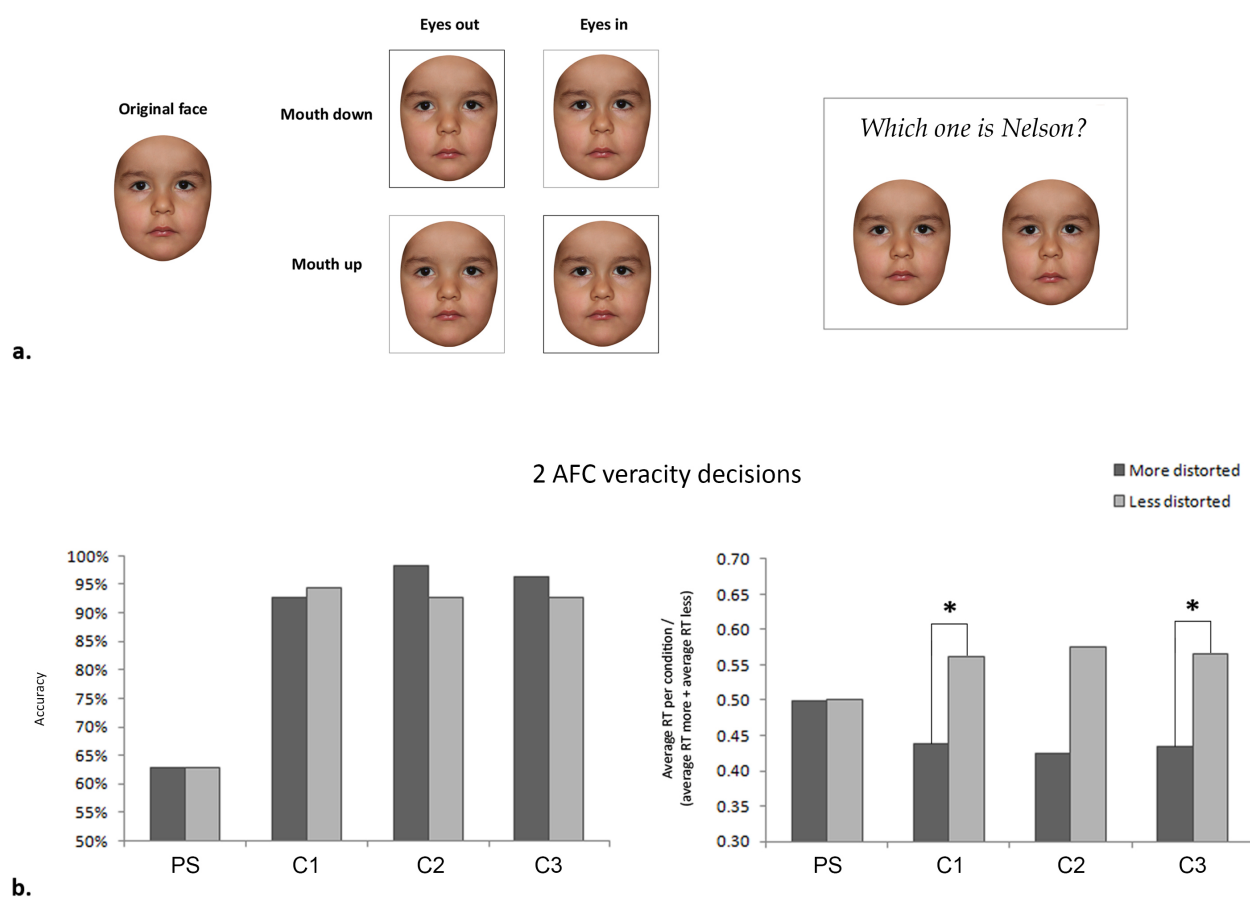


Figure 8. Stimuli and results for Experiment 7: Representation of Overall Facial Geometry. **a.** Examples of stimuli created from an original face (left), which were manipulated in that their original configuration was maintained (“less distorted”; dark rectangles) or altered (“more distorted”; light rectangles). An example of a trial is displayed on the right; here the original face is paired with a more distorted version (eyes in, mouth down). **b.** Subjects accuracy scores and RT indices for veracity decisions between original and modified face stimuli depending on type of distortions; asterisks indicate significant differences between conditions for individual subjects’ RTs.

together ($t=26.58$, $p<.001$). Across all participants, accuracy did not vary as a function of distortion type. Crawford and Garthwaite’s (2002)’ RSDT indicated significant differences between the two conditions for PS, as opposed to controls ($t_2=10.69$, $p<.005$). As evident from Figure 8b this reflects the fact that two controls’ accuracy scores were slightly higher for more, as compared to less distorted trials, whereas PS’s accuracy scores did not vary as a function of type of distortion.

As expected, PS took much longer than controls overall ($t=4.54$, $p<.05$). RTs of two controls differed significantly between conditions. Specifically, all controls responded faster for trials on which original faces were presented with more distorted ones (C1: $t_{96}=1.84$, $p<.05$; C2: $t_{98}=.35$, ns ; C3: $t_{98}=1.70$, $p<.05$). For PS on the other hand, no such difference was found ($t_{63}=.15$, ns). If anything,

her RTs were relatively prolonged for the more, as compared to less distorted condition. Crawford and Garthwaite’s (2002) RSDT confirmed that the pattern displayed by PS differed significantly from that obtained for control participants ($t_2=8.86$, $p<.05$), which is clearly demonstrated by participants RT indices displayed in Figure 8b.

Discussion

Again, this experiment yielded markedly different performance patterns for healthy controls and PS. Our assumption was that extraction of the overall, global facial configuration would facilitate performance and give rise to a benefit for detection (and rejection) of more distorted versions of a given face. Indeed, controls were all significantly faster at discriminating between original faces, and faces in which the facial configuration had been altered (more distorted), as compared to preserved (less distorted). The pattern of

performance displayed by three healthy controls is in line with the findings of Barton et al. (2003) and Ramon (2015a). Thus, it reflects a mode of holistic processing found only for observers who have a representation of the overall facial configuration of the face identities presented simultaneously (note that this effect does not arise in personally familiar observers in a *delayed matching* task, which to our knowledge has not been tested using unfamiliar face stimuli). In contrast, given the absence of a benefit for more, over less distorted faces, PS's results clearly indicate that she does not appreciate the overall facial configuration as controls do, supporting the outcome of the previous experiment with the composite face effect (experiment 5) and whole-part face effect (experiment 6).

Experiment 8: Recognition of Intact and Shuffled Face Parts

Rationale

In this experiment, we aimed to further investigate the view that PS processes individual faces piece-by-piece rather than a single integrated unit. To do so, we created new stimuli from the original face pictures by first cleanly removing all external features, so that the faces contained only the main internal features at high contrast, without texture information (Figure 9a). Then, we created shuffled versions of these faces, by exchanging the position of the four parts (two eyes, mouth, nose) in order to disrupt the facial configuration (Figure 9a). With these stimuli, we tested PS's and control participants' ability to assign the appropriate names of personally familiar children to either configurally intact faces, or their respective shuffled versions. We hypothesized that normal observers would show superior performance when facial parts are presented in their intact as opposed to shuffled configuration. In keeping with the idea that PS utilizes the constituent parts in isolation to recognize personally familiar faces, we hypothesized that her performance would not – or less – be determined by the intactness of the overall facial configuration.

Stimuli and Procedure

We selected 24 of the children's cropped pictures used in the previous experiments (16 females). Using Adobe Photoshop 7, we increased the contrast and the brightness of each picture in order to isolate the internal features of the face (see Figure 9a). For stimuli with normal configuration, the inter-feature spatial relations were identical to those of the original faces; to create the stimuli with shuffled configuration, each of those with normal configuration was modified in a specific manner (novel location of facial features as shown in Figure 9a, resulting in a total of 48 stimuli, subtending on average $6.6 \times 8.1^\circ$ of VA). In a 2AFC paradigm, subjects were presented with a name for 1 second. After a 400 ms ISI, two faces were presented side-by-side for unlimited time (either both in normal or shuffled configuration), with participants having to identify the target item belonging to the previously seen name. Each stimulus was presented four times in total across 8 blocks of 24 stimuli each. Configuration types were presented interleaved and in blocks (normal and shuffled configuration for odd and even blocks, respectively). Order of presentation within each block was fully randomized; stimuli were presented using E-prime 1.1.

Results

The results of PS and her age-matched controls are shown in Figure 9b and reported in Table 7. Both controls exhibited high accuracy rates for both conditions, between which no significant differences were found (C1: $\chi^2_1 = .87$, *ns*; C2 achieved 100% in both conditions). However, controls were much slower for shuffled face parts (C1: $t_{170} = 4.74$; $p < .001$; C2: $t_{180} = 3.88$; $p < .001$). PS performed this task at an acceptable level of performance, even though she was slower than both controls. However, contrary to controls, neither PS's accuracy, nor RTs differed as a function of condition (Figure 9b; $\chi^2_1 = 1.51$; *ns*; $t_{156} = .08$; *ns*).

Discussion

The results of Experiment 8 reinforce the view that PS does not benefit from an intact facial

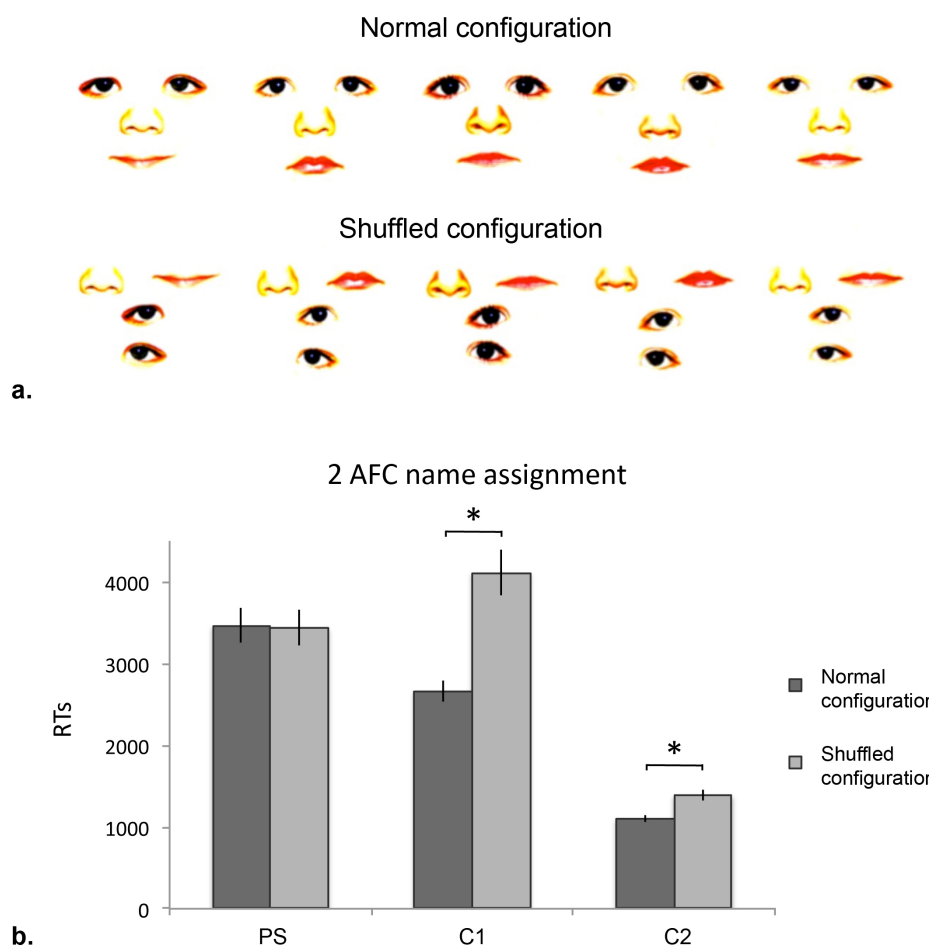


Figure 9. Stimuli and results for Experiment 8: Recognition of Intact and Shuffled Face Parts. a, Examples of stimuli created to present facial features in their original, or shuffled configuration. b, Subjects' RTs (with standard errors) across conditions with asterisks indicating significant differences.

configuration of the constituent parts when required to process personally familiar faces. Both with respect to accuracy and RTs, her performance was uninfluenced by shuffling the individual facial features. In sharp contrast, although both age-matched controls were able to recognize personally familiar faces from their shuffled versions, they were significantly faster when the respective parts were presented in their original, i.e. veridical, configuration.

Experiment 9: Breaking Apart the Eye Region

Rationale

In the final set of experiments we aimed to provide a stringent test of the impairment in holistic processing of the prosopagnosic patient PS, using only the eye region as stimulus, guided by the following rationale. In the face processing literature, holistic processing is sometimes misunderstood as a process that concerns the whole face, or even requires the

presence of a whole face stimulus (e.g., Leder & Bruce, 2000; Rakover, 2012; Rakover & Teucher, 1997). However, the term “holistic/configural” reflects a *process*, i.e. *the simultaneous integration of the parts of a face into a single representation*, which does not necessitate the presence of the whole face stimulus. That is, this process can potentially be applied to part of a face, for instance an occluded face, allowing completion of the representation. Hence, as long as more than one part is present in the stimulus, for instance a *pair* of eyes, holistic processing is at play and can influence performance (see Rossion, 2008; 2013 for an in depth discussion of this issue). Following this rationale, we designed a set of experiments in which we used the region of the eyes alone, a region that forms a configuration itself, comprising the two eyes (here without eyebrows; see Figure 10). The advantage of using only this region is that there is no

ambiguity as to the nature of the diagnostic information to use across the whole face, and no issue of a differential fixation and attentional pattern between the patient and the controls: information can only be extracted from the eyes region. Then, we applied a number of stimulus manipulations to information conveyed by this eye region in order to disrupt the original configuration of its constituents: isolation of one eye, inversion, or vertical misalignment of the eyes. We anticipated that controls' performance would be detrimentally affected by these manipulations. PS's performance, on the other hand, should be comparably less affected by such manipulations. We also added a manipulation that preserved the original configuration but reduced local diagnostic information, i.e. by removing color information, the hypothesis being that PS would be relatively more affected by this manipulation.

Stimuli and Procedure

For the present experiment we used a subset of the 27 x 2 familiar feature stimuli ("parts") created for experiments 4 and 6. For each subtest, the stimuli used here—depicting eyes without eyebrows—were modified according to the question to be addressed (see Figure 10 for examples of the stimuli). Color features and their gray-scaled equivalents were used in Experiment 9a; the remaining experiments involved gray-scaled stimuli. In Experiment 9b, we sought to address whether participants' recognition of the eyes of familiar individuals requires information from this region as a whole. Therefore, we presented stimuli that contained either both eyes, or only the (individuals') right one (left eye from the observers' perspective). Then, we also investigated holistic processing of the eye region using upright and inverted (experiment 9c), as well as intact or vertically misaligned eyes (experiment 9d). For all four subtests, participants performed forced-choice name assignments. Each trial began with presentation of a child's name for 100ms. After a 400ms ISI, two test stimuli were presented

until participants responded which of them corresponded to the previously presented name; trials were separated by a 1000ms ISI. The experimental conditions were presented at random and twice per identity (to counterbalance for correct response side). The number of trials for each experiment was 54 (response side x identity) times the number of conditions included. Analyses were conducted on both behavioral measures where possible (i.e., when accuracy was not at ceiling, or differed across conditions).

Results

Experiment 9a: Isolation of the eyes. The results of Experiment 9a are provided in Table 8a and Figure 10a. Participants' accuracy rates were unaffected by isolation of the eye(s) (both C1 and C2 made two mistakes for isolated eyes: $\chi^2_1=2.04$, $p>.05$; PS: $\chi^2_1=.05$, ns) but their correct RTs increased significantly (C1: $t_{101}=3.15$, $ps<.0001$; C2: $t_{102}=1.71$, $p<.05$). PS scored well above chance in this task (75%, $p<.0001$), without any difference between conditions ($\chi^2_1=.05$, ns). With respect to correct RTs, PS exhibited the opposite pattern, i.e., responded faster for trials on which a single, as opposed to both eyes were presented, albeit not significantly ($t_{78}=-1.37$, ns).

Experiment 9b: Stimulus inversion. The results of Experiment 9b are provided in Table 8b and Figure 10b. C2 was at ceiling for both conditions but C1 was significantly more accurate for upright as compared to inverted stimuli ($\chi^2_1=7.05$, $p<.005$). PS scored above chance level (66%, $p<.05$) but without any effect of orientation ($\chi^2_1=.04$, ns). While both controls' RTs were significantly shorter for upright as compared to inverted stimuli (C1: $t_{94}=3.63$; C2: $t_{103}=4.08$; $ps<.0001$), PS's correct RTs did not vary across conditions ($t_{69}=1.83$, ns).

Experiment 9c: Vertical misalignment of the eyes. The results of Experiment 9c are provided in Table 8c and Figure 10c. Both controls performed at ceiling across conditions; PS performed above chance level (69%, $p<.005$) but her accuracy rates did not vary as a function of vertical misalignment ($\chi^2_1=.23$, ns).

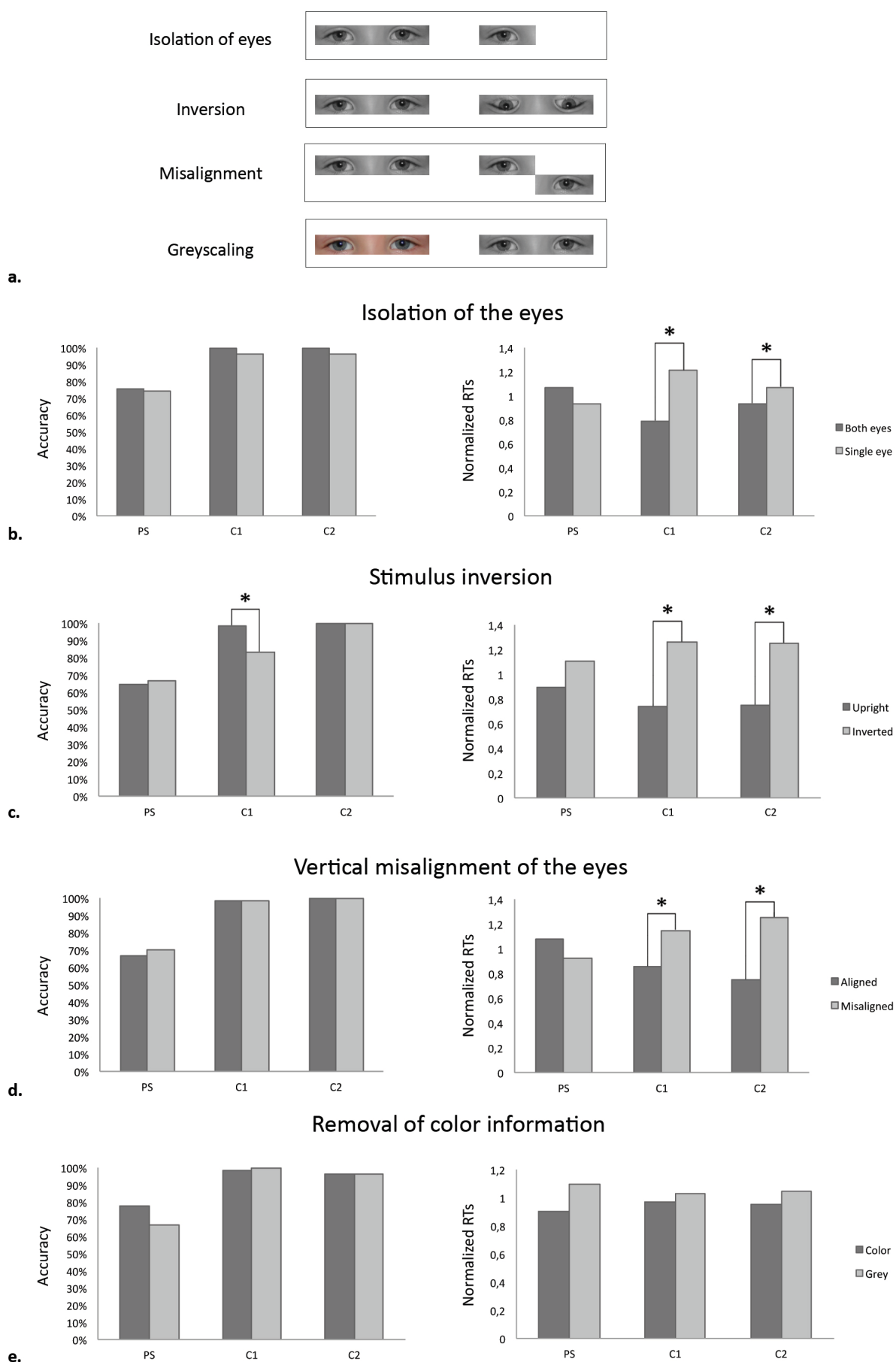


Figure 10. Stimuli and results for Experiment 9: Breaking Apart the Eye Region. a, Stimuli differed with respect to the information contained or manipulated, respectively. b – e, display subjects' performance across the subtests of experiment 9.

Regarding RTs, both controls displayed significantly prolonged RTs for vertically misaligned as compared to aligned the eyes (C1: $t_{102}=2.71$; C2: $t_{104}=3.90$, $ps<.005$). In contrast, PS responded faster for misaligned eyes, albeit not significantly ($t_{71}=-1.55$, ns).

Overall, the results of these three experiments indicate that the region of the eyes forms a configuration in itself: when it is compartmentalized through misalignment or isolation, or presented in a non-typical orientation (i.e., inverted), typical observers perform less well at identifying this facial information. In stark contrast, and in line with our predictions, PS is unaffected by these stimulus manipulations. To ascertain that it is indeed an impairment of holistic processing underlying the pattern observed for PS as opposed to healthy controls, Experiment 9d was conducted. The rationale was that removal of color information from the otherwise intact eye region should lead to no performance decrease in controls, in contrast to a substantial performance decline in PS.

Experiment 9d: Removal of color information. The results of Experiment 9a are provided in Table 8a and Figure 10b. Both controls performed at ceiling with C2 making only one mistake (ceiling performance). Regarding RTs, neither of the controls exhibited an effect of color removal (C2: $t_{103}=1.00$; C1: $t_{103}=1.01$, $ps\ ns$). PS also performed above chance level (72.5%, $p<.0005$). Comparing her performance across conditions reveal no significant difference, neither for accuracy scores nor RTs ($\chi^2_1=1.66$; $t_{77}=1.23$, $ps\ ns$). This indicates that here, contrary to the previous experiments where PS utilized color information, PS's behavior was not significantly affected by removal of color information in this (sub)experiment.

Discussion

As expected across all subtests of experiment 9 PS's performance was inferior to that of normal controls, but above chance level. However, in contrast to controls, her performance was relatively stable across conditions involving disruption of the original

configuration. For instance, while controls' performance decreased when only a single eye, as compared to both eyes, was present, PS's performance was unaffected. This pattern was also observed when the eyes were vertically misaligned. With inversion PS's RTs increased; however, this increase was modest compared to the performance change observed for controls. Contrariwise, controls' performance was virtually unaffected by removal of surface information including color, while PS's performance declined much more for these conditions, albeit not significantly. Hence, across a series of manipulations applied to a specific part of the face (i.e., the eye region), we observed a dissociation between the prosopagnosic patient and typical observers: her impairment affects in particular processing of the eye region. These observations shed light on the nature of the deficient process in this pure case of prosopagnosia.

General Discussion

In nine main behavioral experiments (17 experiments in total), we evaluated the acquired prosopagnosic patient PS's (in)ability to process a large set of pictures of faces that she had been extensively exposed to in real life, shedding light on the kind of information and the nature of the processes that are preserved/impaired in this unique case of acquired prosopagnosia.

Overall, our findings show that PS's recognition of highly familiar 3-4 year-old children of her kindergarten is severely impaired – both in terms of accuracy and speed (experiments 1 and 2). Most importantly, her performance also differs qualitatively from the only other people comparably familiar with these children's faces, i.e., her colleagues. Specifically, PS relies relatively more on external features, color and local details of faces and is also particularly impaired at processing the eye region of the face, as shown previously with unfamiliar faces with this patient (Caldara et al., 2005; Orban de Xivry et al., 2008), and other cases of acquired prosopagnosia (Bukach et al., 2006; 2008; Barton, 2008b; Pancaroglou et al., 2016).

Specifically, in experiments 3 and 4, we demonstrated this reduced sensitivity to the socially crucial and normally highly diagnostic eye region for personally familiar faces. In experiment 3, we tested PS in an original response classification experiment with randomly placed windows revealing only circumscribed local information (“Bubbles”) of the personally familiar faces. In line with previous observations made with experimentally learned unfamiliar faces (Caldara et al., 2005), PS relied much more on the mouth than the eyes, thereby exhibiting an atypical pattern of information use, which was moreover remarkably stable throughout the entire experiment (more than 20,000 trials). A 2-alternative face matching task, as well as a familiar face recognition task performed with pre-defined isolated parts in experiment 4 also supported these findings. Altogether, these observations indicate that the same impairment observed previously with unfamiliar faces is associated with a deficient long-term representation of the eye region of personally familiar individuals’ faces in prosopagnosia.

Finally, the results of experiments 5 to 8 highlight PS’s inability to represent the multiple parts of the face as a single unit. This impairment of holistic face processing (McKone et al., 2003; Tanaka & Farah, 1993; 2003; Rossion, 2008; 2009; 2013), is considered to be at the root of her difficulty at processing a facial region constituted of multiple features, such as the eyes (Caldara et al., 2005; Orban de Xivry et al., 2008; Rossion, 2014). Experiment 9 supports this view, showing that contrary to controls, PS’s processing of a pair of eyes is unaffected by breaking this local configuration in two pieces.

Altogether, these observations do not only strengthen our understanding of PS’s case and the neuropsychological impairment of prosopagnosia following brain damage in general, but also strongly suggest that acquired prosopagnosia affects unfamiliar and familiar face processing in a qualitatively identical way.

Weaknesses and Strengths of this Study

Obviously, this investigation is atypical, and is inherently limited by a number of factors. First, only one patient with prosopagnosia could be tested. However, we argue that the patient PS is a particularly diagnostic case, for several reasons. First, her impairment is limited to the category of faces, with object recognition being preserved, including fine-grained discrimination of complex unfamiliar and familiar shapes (Busigny et al., 2010b). Such a pure prosopagnosia following brain damage is rare, and particularly important to isolate the nature of the deficient process. Second, this case has been studied extensively, described in numerous published behavioral and neural studies, and is, to our knowledge, the most thoroughly documented case of acquired prosopagnosia in the scientific literature (Rossion, 2014). Also, PS is willing to give her time for extensive investigations, and able to understand and perform complex behavioral tasks. Finally, and perhaps most importantly, she was professionally active as a kindergarten teacher, and hence was heavily exposed to a large set of homogenous faces, which she *had to identify and recognize* in real life. This makes PS a truly unique case of acquired prosopagnosia for the kind of study reported here.

A second issue is that our control sample was heavily constrained: PS only had two colleagues, with only one being age-matched, and we were fortunate to be able to test both of them. Nonetheless, to strengthen our observations, we managed to test a third control (C3) for some experiments, although she was much less familiar with the faces (having substituted PS or her colleagues on a few occasions in the kindergarten). Notably, C3 showed performance patterns that paralleled those of PS’s full-time colleagues C1 and C2. We would like to emphasize that PS’s half-time (compared to her colleagues’ full time) occupation in the kindergarten throughout the year (i.e., 2.5 days per week) cannot at all account for the pattern of results observed in the study. Indeed, as mentioned earlier, in this real life learning and

familiarization context, the level of exposure and attention on the children's faces is uncontrolled: subjects are free to pay as much attention as they want or need to encode the children's faces in memory. In fact, PS always reported that she had to spend much more time than her colleagues paying attention to the children's physical characteristics, including their faces, in the kindergarten, and that she systematically, and spontaneously, studied a number of features about the children during the year in order to avoid recognition failures. Moreover, throughout our experiments, PS was exposed to the face pictures much more than the controls, e.g. she completed 21,600 Bubbles trials (compared to 2160 trials completed by C1; C2 did not participate in experiment 3), as well as many refresher sessions. Finally, our approach of employing numerous and various stimulus manipulations and paradigm, alongside systematically varying task demands effectively mitigated the issue of a limited number of control subjects. Essentially, PS could serve as her own control, considering the dissociations between her performance across the different conditions. In this context of a single-case approach in neuropsychology (Caramazza, 1986; Shallice, 1988), it is also important to emphasize the need to accumulate congruent evidence across many experiments as in the present investigation.

A particular strength of this study, which we would like to emphasize, is the richness of the stimulus set, its visual homogeneity and the robustness of familiar face representations in memory. Unlike various paradigms involving unfamiliar face processing, for which significant effects typically emerge at the level the group, but not at the single-subject level, our control participants generally exhibited clear and large effects, thereby providing an excellent comparison against PS's performance patterns. For instance, the composite face effect and whole-part advantage (experiments 5 & 6), which are not always exhibited by all individuals and can be weak in some participants when tested with unfamiliar faces

(Ramon et al., 2010; Michel et al., 2006; Avidan et al., 2011), were very large for each control reported here. Hence, the absence of these effects for the patient PS in the present study is truly informative.

Given to the robustness of personally familiar face recognition, and the unlimited duration with which stimuli were presented, controls performed at ceiling for several experiments that were nevertheless challenging and informative when tested on PS. While controls' ceiling performance prevented statistically meaningful comparisons between conditions in terms of accuracy scores, this was not the case for PS, and controls' correct RTs were all the more meaningful. Additionally, to address the issue of ceiling effects, we implemented additional tasks throughout (e.g., forced-choice name assignment, familiarity decisions) that were anticipated to lower controls performance to reveal potential differences between conditions for their accuracy scores. Due to the nature of PS's deficit, however, this at times led to her exhibiting chance level performance.

Finally, for obvious reasons, we were not able to test PS's recognition of faces learned *before* her accident. Thus, the present investigation concerned the faces of people who became personally familiar to the patient only after her brain injury, and its conclusions may not be valid for her representations of faces learned before she became prosopagnosic. However, PS's behavior in the kindergarten indicates that she had become highly familiar with these faces, as evidenced also by her performance in experiment 1, where she achieved a reasonable score for the pictures with (and even without) external features. Moreover, like other cases of prosopagnosia reported in the literature, PS's face recognition impairment reportedly concerns recognition of faces of individuals who were familiar before, as well as those who became familiar after her injury (see Tippett et al., 2000 for a patient with a specific impairment at learning new faces).

PS's Performance at Recognizing Familiar Faces in Real-life Settings

Overall, our experiments consistently demonstrate that PS's performance at identifying and recognizing individuals based on their facial information was inferior to that of her colleagues (both in terms of accuracy, and RTs). This also includes the very first experiment, in which she was presented with natural photographs of the children's faces.

Naturally, this raises the question of how PS managed to deal with the problem of (rapidly) recognizing the children in real life, i.e., in the context of the kindergarten. Actually, in this context, since her accident, neither PS nor her colleagues ever reported any recognition problem. PS always identified the children in the kindergarten correctly, and several authors of this paper also noticed that PS had no problem of identification during a number of visits in the kindergarten. Only when she was confronted with a child from a different kindergarten, PS attempted to bring the child inside her kindergarten—an obvious case of misidentification.

This anecdote concurs with the observation that, when faced with ambiguity, namely when familiar and unfamiliar faces are mixed in a set and she has to identify the familiar faces, her performance can be close to chance level (Busigny & Rossion, 2010). However, in the context of the kindergarten in real life, she had to deal with a limited set and distinguish the members of this known set of children only. Nevertheless, PS has always acknowledged that her professional activity became extremely tiring since her accident because she could not readily identify the children's faces as she was able to prior to having sustained brain damage. Instead, she continuously needed to concentrate in order to encode and recall a vast amount of information to compare against the individual with which she was confronted. She would use e.g. their face features, haircut, size, play habits (e.g., usual location in the kindergarten, preferred toys), their voice, the body shape and posture, etc. This was precisely the reason that PS proceeded to work only half

time since her accident—not because of any other physical or neuropsychological impairment.

Thus, our findings highlight that the contextual setting provides a powerful means to restrict PS's laborious search: knowing that her 27 kindergarten pupils were presented in our identification tasks dramatically improved her quest for the facial information that is diagnostic of a given identity. Two additional findings support the idea that top-down knowledge can afford reliable (albeit prolonged) performance. In their seminal study, Rossion et al. (2003) reported that PS was not able to reliably distinguish above chance level famous from unfamiliar individuals: she responded “familiar” to only 14 of 60 famous faces presented, and was only able to correctly verbally identify four of these. This is plausible, as determining the familiarity of a famous/unfamiliar face can involve presentation of faces drawn from a virtually unlimited pool of potential identities. Here, we observed that, although slower than controls, PS could recognize the children's faces, and her performance increased with decreasing numbers of individuals presented (e.g., 27 vs. 16 in Experiments 1 and 2, respectively). Finally, PS can also achieve acceptable levels of performance in terms of accuracy in the context of unfamiliar face matching tasks. Ramon and Rossion (2010) reported that PS's performance varied dramatically, depending on whether she was provided information about which facial feature was diagnostic. Specifically, her overall performance profile resembled that of healthy controls when instructed to attend the task-relevant information, i.e. when she was certain as to which feature could be used to discriminate between the face stimuli.

Apart from her quantitative impairment at face recognition, our experiments completely confirmed the observations made on PS with tests involving unfamiliar faces. First, contrary to normal observers, she performed better with the mouths than the eyes of personally familiar faces. Furthermore, her performance was

affected by removal of external features and surface cues, such as color and texture, and she identified individual faces part by part, due to an inability of integrating the parts into a unified representation (i.e., holistic processing). These observations are not merely a confirmation of previous studies—here they were made in experiments requiring the comparison of a face stimulus to a representation stored in memory, rather than simultaneous or delayed comparison of 2D images of unfamiliar faces. Moreover, this memory is based on real-life experience, not only the learning of 2D images of unfamiliar faces. Thus, the results of the experiments performed in this study suggest that PS has encoded individual children's faces as a collection of independent parts, with an emphasis on the mouth. Hence, when she has to compare a displayed part of a face to her representation in memory, she is not influenced—positively or negatively—by the presence of the other parts of the stimulus and their relative distance to the target part (experiments 5 to 8). As we have argued in previous reports, this behavior seems to be a common feature of many cases of acquired prosopagnosia (Davidoff et al., 1986; Levine & Calvanio, 1989; Sergent & Villemure, 1989; Spillmann et al., 2000; Saumier et al., 2001; Boutsen & Humphreys, 2002; Barton et al., 2002; Riddoch et al., 2008; Wilkinson et al., 2009; Busigny et al., 2010b), who can nevertheless greatly vary in terms of the severity of their disorder and additional neuropsychological defects (Busigny et al., 2014; Rossion, 2014).

No Qualitative Difference Between Personally Familiar and Unfamiliar Face Processing in Acquired Prosopagnosia

Our observations strongly suggest that familiar and unfamiliar faces are initially handled by means of the same critical process: the integration of the face parts into a holistic representation. At first glance, this view may appear to contradict the proposal that familiar and unfamiliar faces are processed in a qualitatively different manner (Tong & Nakayama, 1999; Knappmeyer et al., 2003;

Megreya & Burton, 2006; Balas et al., 2007; Carbon, 2008; Watier & Collin, 2009; Gobbini et al., 2013; Visconti di Oleggio Castello et al., 2014; for a discussion see Ramon et al., 2011; Ramon, 2015a; 2015b; Ramon & Gobbini, submitted). However, it may be that holistic encoding is only an early necessary step, followed by qualitatively different processes for familiar and unfamiliar faces emerging with real-life experience. That is, it remains unclear whether or not this *initial* processing is modulated through experience in healthy observers, or whether familiarity-related processing differences arise only at later stages due to the multiple levels of representations (visual, semantic) available for familiar faces.

Regardless, PS could utilize other information that healthy observers do not typically tend to use, e.g. that a given child has blue eyes (in experiments where color information was available), thin lips, etc. Additionally, while her ability at processing facial information is clearly impaired, PS could also utilize non-visual identity-specific information in a top-down manner to effectively determine and personally familiar individual's identity. In the present study we only addressed the efficiency with which identity-specific *visual* information would affect her processing. Further studies are required to determine whether the compensatory strategies she engages in in every-day life may actually enhance her abilities in other domains, such as processing of voice, gait, or posture.

In summary, we provide converging evidence across a large set of experiments performed in a single neuropsychological case that processing of personally familiar faces is affected in a similar manner as that of unfamiliar faces in acquired prosopagnosia.

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TABLES

Table 1. Performance (accuracy and correct RTs) for Experiment 1: Familiar Face Identification.

	Accuracy (% correct)		RTs in ms (SD)	
	All features available	Cropped, gray-scaled faces	All features available	Cropped, gray-scaled faces
PS	87	46	7458 (4302)	12355 (8192)
C1	96	96	3448 (1910)	2708 (1088)
C2	98	100	2721 (717)	2808 (839)
C3	91	91	4297 (2733)	4064 (2634)

Table 2. Performance (accuracy and correct RTs) for Experiment 2: Identification of Anti-Caricatures.

	Accuracy (% correct)					RTs in ms				
	Amount of identity information					Amount of identity information				
	100 %	80 %	60 %	40 %	20 %	100%	80%	60%	40%	20%
PS	75	83	83	73	30	6178	7888	8056	11111	18635
C1	100	100	100	100	94	1456	1588	1475	2105	4041
C2	100	100	100	100	88	966	952	1005	1305	2720

Table 3. Performance (accuracy and correct RTs) for Experiment 4: Recognition of Isolated Features. Behavioral results are provided separately for **a.** verbal identification and **b.** 2AFC name assignment for eyes and mouth stimuli, respectively.

a.	Verbal identification			
	Accuracy (% correct)		RTs in ms (SD)	
	Eyes	Mouth	Eyes	Mouth
PS	15	52	14493	14098
C1	74	52	2619 (1799)	8422 (9667)
C2	93	81	3828 (2808)	6038 (5651)
C3	81	44	3026 (1780)	7330 (6432)
b.	2 AFC name assignment			
PS	76	87	5641	4285
C1	100	93	2007 (651)	2377 (976)
C2	100	98	1723 (712)	2113 (996)
C3	100	98	2227 (1320)	2581 (1229)

Table 4. Performance (accuracy and correct response times) for Experiment 5: Composite Face Effect. Individual subjects' performance is provided separately for **a.** Verbal identification (experiment 6a), **b.** name assignment (experiment 6b) or **c.** familiarity decisions (experiment 6c) based on top parts of composite stimuli when aligned, or misaligned with task-irrelevant bottoms.

a. Verbal identification				
	Accuracy (% correct)		RTs in ms (SD)	
	Aligned	Misaligned	Aligned	Misaligned
PS	14	8	20423 (15582)	16519 (8300)
C1	86	94	2760 (1960)	1707 (710)
C2	82	98	2229 (1006)	1761 (397)
b. Forced-choice name assignment				
PS	68	71	5413 (3213)	5215 (2431)
C1	99	97	2236 (1239)	1625 (489)
C2	96	99	1226 (328)	1102 (246)
c. Forced-choice familiarity decisions				
PS	82	64	2916 (1288)	3062 (1282)
C1	82	98	1166 (646)	765 (231)
C2	100	100	982 (358)	815 (141)

Table 5. Performance (accuracy and correct RTs) for Experiment 6: Whole-Part Advantage. Results are provided for both **a.** forced-choice name assignment and **b.** familiarity decisions, separately for task-relevant features (eyes, mouths).

a. Forced-choice name assignment to eyes				
	Accuracy (%)		RTs in ms (SD)	
	Wholes	Parts	Wholes	Parts
PS	82	80	4493 (2852)	3087 (1850)
C1	96	98	1513 (485)	1847 (802)
C2	100	100	1052 (290)	1232 (492)
Forced-choice name assignment to mouths				
PS	82	78	4472 (2255)	4652 (2560)
C1	96	94	1557 (645)	2237 (1270)
C2	100	100	1070 (381)	1455 (759)
Forced-choice familiarity decisions based on eyes				
PS	69	61	551 (7270)	8440 (4046)
C1	100	85	578 (575)	3329 (2786)
C2	100	93	93 (1530)	3048 (1826)
Forced-choice familiarity decisions based on mouths				
PS	87	72	26 (4161)	4699 (1709)
C1	94	76	59 (1067)	2573 (1640)
C2	100	98	158 (316)	1729 (791)

Table 6. Performance (accuracy and correct RTs) for Experiment 7: Representation of Overall Facial Geometry. Forced-choice veridicality decisions between original and altered (more and less distorted) facial configurations.

	Accuracy (% correct)		RTs in ms (SD)	
	More	Less	More distorted	Less distorted
PS	63	63	14298 (9499)	14333 (10106)
C1	93	94	2746 (1869)	3506 (2057)
C2	95	93	2048 (988)	2782 (2754)
C3	96	93	5359 (3528)	6957 (4549)

Table 7. Performance (accuracy and correct RTs) for Experiment 8: Recognition of Intact and Shuffled Face Parts. 2AFC name assignment of facial features presented in their veridical (normal) or shuffled configuration.

	Accuracy (% correct)		RTs in ms (SD)	
	Normal configuration	Scrambled	Normal configuration	Scrambled
PS	89	82	3462 (1937)	3437 (1857)
C1	96	93	2662 (1176)	4113 (2584)
C2	100	100	1101 (363)	1388 (602)

Table 8. Performance (accuracy, correct RTs) for experiment 9: Breaking Apart the Eye Region.

	Accuracy (% correct)		RTs in ms (SD)	
	Both eyes	Isolated eye	Both eyes	Isolated eye
a.	Isolation of the eyes			
PS	76	74	4142 (2106)	3600 (1314)
C1	100	96	2503 (1214)	3823 (2777)
C2	100	96	1611 (732)	1841 (632)
b.	Stimulus inversion			
	Upright	Inverted	Upright	Inverted
PS	65	67	4461 (2248)	5498 (2513)
C1	98	83	2807 (1535)	4786 (3561)
C2	100	100	1417 (409)	2345 (1602)
c.	Vertical misalignment of the eyes			
	Eyes intact	Eyes misaligned	Eyes intact	Eyes misaligned
PS	67	70	4297 (1796)	3691 (1540)
C1	98	98	2459 (1232)	3289 (1836)
C2	100	100	1273 (341)	2132 (1567)
d.	Removal of color information			
	Color	Greyscaled	Color	Greyscaled
PS	78	67	3637 (1471)	4407 (2263)
C1	96	96	2662 (1321)	2938 (1431)
C2	98	100	1442 (444)	1529 (451)