Does Prosopagnosia Take the Eyes Out of Face Representations? Evidence for a Defect in Representing Diagnostic Facial Information following Brain Damage

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Abstract

■ One of the most impressive disorders following brain damage to the ventral occipitotemporal cortex is prosopagnosia, or the inability to recognize faces. Although acquired prosopagnosia with preserved general visual and memory functions is rare, several cases have been described in the neuropsychological literature and studied at the functional and neural level over the last decades. Here we tested a brain-damaged patient (PS) presenting a deficit restricted to the category of faces to clarify the nature of the missing and preserved components of the face processing system when it is selectively damaged. Following learning to identify 10 neutral and happy faces through extensive training, we investigated patient PS's recognition of faces using Bubbles, a response classification technique that sampled facial information across the faces in different bandwidths of spatial frequencies [Gosselin, F., & Schyns, P. E., Bubbles: A technique to reveal the use of information in recognition tasks. *Vision Research, 41*, 2261–2271, 2001]. Although PS gradually used less information (i.e., the number of bubbles) to identify faces over testing, the total information required was much larger than for normal controls and decreased less steeply with practice. Most importantly, the facial information used to identify individual faces differed between PS and controls. Specifically, in marked contrast to controls, PS did not use the optimal eye information to identify familiar faces, but instead the lower part of the face, including the mouth and the external contours, as normal observers typically do when processing unfamiliar faces. Together, the findings reported here suggest that damage to the face processing system is characterized by an inability to use the information that is optimal to judge identity, focusing instead on suboptimal information. ■

INTRODUCTION

In humans, faces convey at a glance a great deal of information (e.g., person's identity, gender, mood, ethnical origin, age) that is crucial for efficient social interactions. A long-standing goal of the face processing research agenda has been to identify which cues are extracted from a face in order to categorize it (according to its gender, expression, identity, race, etc.). In other words, what is the diagnostic (i.e., most useful) information that is extracted from faces, and how does it vary according to the task at hand? To address this issue, various methods have been used, such as categorizing faces presented with masked or isolated facial features (e.g., Bruce, Burton, et al., 1993), with surface and shape properties separated (Hill, Bruce, & Akamatsu, 1995), with only information from the principal components of a face set (e.g., Calder, Burton, Miller, Young, & Akamatsu, 2001), and, more recently, by sampling facial information at a fine grain to derive the information subset associated with categorization judgments (Smith, Cottrell, Gosselin, & Schyns, 2005; Sekuler, Gaspar, Gold, & Bennett, 2004; Schyns, Bonnar, & Gosselin, 2002; Gosselin & Schyns, 2001).

Humans are generally considered face processing experts because they efficiently extract the diagnostic cues allowing face categorization, identification, and generalization (Tanaka, 2001; Diamond & Carey, 1986). Yet, several observations illustrate the complexity and difficulty of face categorization. First, the ''expert'' human face processing system of adults undergoes quite a long development, not reaching full maturity before puberty (Campbell, Coleman, et al., 1999; Taylor, McCarthy, Saliba, & Degiovanni, 1999; Carey, 1992). Secondly, the face processing system is not so efficient at processing unfamiliar faces. This is demonstrated by the striking difference between our excellent ability to generalize across different images of familiar faces and our relatively poor performance when performing the

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same task on unfamiliar faces (e.g., Bruce, Henderson, et al., 1999; Burton, Wilson, Cowan, & Bruce, 1999; Young, McWeeny, Hay, & Ellis, 1986), suggesting that the efficiency of face processing arises from robust long-term representations of others' faces.

Possibly the most striking evidence that the extraction of diagnostic information from faces is nontrivial is the observation of patients who have lost this ability, despite no other obvious impairments of the visual system (at least as far as neuropsychological tests demonstrate) and a preserved ability to recognize people through other modalities (e.g., voice). This deficit in face recognition is a spectacular impairment, and despite its rarity (it occurs in less than 1% of brain-damaged patients, Sergent & Villemure, 1989), it has attained considerable notoriety in the neuropsychological literature since the first clinical observations (see Grüsser & Landis, 1991; Quaglino, 1867; Wigan, 1844) and the introduction of the term *prosopagnosia* by Bodamer (1947) (English translation by Ellis & Florence, 1990).

Prosopagnosia generally follows brain damage to bilateral occipitotemporal areas (e.g., Sergent & Signoret, 1992; Farah, 1990; Landis, Regard, Bliestle, & Kleihues, 1988; Damasio, Damasio, & Van Hoesen, 1982). Although able to detect a face among objects (''face detection''), prosopagnosic patients typically lose the ability to identify familiar faces, including famous persons, friends, and relatives, or even their own face (Damasio, 1985). Despite the rarity of prosopagnosic patients with well-preserved visual perception and memory, a number of such brain-damaged cases have been described over the last decades (e.g., Sergent & Signoret, 1992; Farah, 1990; for more recent cases, see Laeng & Caviness, 2001; Gauthier, Behrmann, & Tarr, 1999).

The clinical and anatomical conditions of prosopagnosia have been of great interest to cognitive neuroscientists willing to clarify the neurofunctional mechanisms of normal face processing. Several key findings have been presented. Anatomical descriptions of prosopagnosia support the critical role of the right hemisphere in the occipitotemporal pathway of face processing (Bouvier & Engel, 2004; Sergent & Signoret, 1992; Landis et al., 1988). The double dissociations reported between the ability to perceive unfamiliar and familiar faces (Malone, Morris, Kay, & Levin, 1982), between the recognition of facial expression and facial identity (e.g., Tranel, Damasio, & Damasio, 1988; Bruyer et al., 1983), or between lip reading and face identification (Campbell, Landis, & Regard, 1986) have helped in isolating the different subfunctions in a cognitive architecture of face processing (Bruce & Young, 1986). The study of prosopagnosia at the functional level has also probably initiated (Bodamer, 1947) and fuelled the ''never-ending'' debate about the modularity of face processing (e.g., Gauthier et al., 1999; Farah, Levinson, & Klein, 1995; Damasio et al., 1982).

Despite the theoretical importance of studies of prosopagnosic patients, an important area of research remains largely unexplored. In descriptions of clinical cases, it is usually reported that prosopagnosic patients who rely on nonfacial cues to recognize people (gait, voice, clothes, etc.) still attend to and extract information from faces that is used to recognize people. Yet, these patients appear to have lost the ability to extract and/or build diagnostic representations of other people's faces. What is then the nature of the facial information that brain-damaged prosopagnosic patients extract when processing faces? To put it differently, what is the nature of the missing and preserved components of the face processing system when it is selectively damaged? Answering this question would undoubtedly contribute to functionally characterizing the selective face impairment that is prosopagnosia, and from there on providing a better understanding of functional aspects of the normal, ''expert,'' face processing system.

However, several limitations may hamper a better understanding of the functional aspects of face processing in prosopagnosia. First, cases of prosopagnosia described in the literature usually suffer from many low-level and high-level visual deficits besides their face impairments: loss of visual acuity, visual field defects (hemianopia, upper visual field problems, or left quadrantopsia generally; for reviews, see Barton, 2003; Goldsmith & Liu, 2001), achromatopsia (about 60% of overlap, Bouvier & Engel, 2004), or difficulties at general configural processing and object recognition (e.g., Gauthier et al., 1999; Sergent & Signoret, 1992; Levine & Calvanio, 1989). Consider, for instance, LH, a patient initially presented with a disproportionately large deficit with face compared to object processing, performing even in the normal range for subtle discrimination tasks on nonface objects such as pairs of glasses (Farah, Levinson, et al., 1995). Other studies revealed that LH had clear deficits at performing visual discrimination tasks on complex patterns and at recognizing nonface objects (e.g., Farah, McMullen, & Meyer, 1991; Levine & Calvanio, 1989; Levine, Calvanio, & Wolf, 1980). Crucially, his recognition failures proved to be more pronounced for certain categories than others (e.g., living vs. nonliving, Farah, McMullen, et al., 1991), and previous studies had concluded that the deficits were due to general factors such as the loss of configural information processing (Levine & Calvanio, 1989). Although these deficits may not explain fully the face recognition impairment observed in these patients, they are likely to affect and modify the strategies that the patient uses when processing faces. A trivial example is that of a prosopagnosic suffering from achromatopsia, who will be unable to use eyes or hair color to recognize or discriminate between people. For these reasons, it is inherently difficult to establish the functional aspects that are specific to the face impairment in prosopagnosia when associated deficits are likely to present confounding factors.

Any attempt to clarify the components (missing and preserved) of prosopagnosia is confronted with the problem of defining the information cues to perform various (face) categorization tasks. A typical strategy is to hypothesize a priori that certain facial cues are not properly processed in prosopagnosia and test this hypothesis by selectively manipulating these cues. This approach may provide interesting outcomes but is inherently limited because faces vary according to a large number of dimensions (Valentine, 1991). By selecting a priori a subset of this information for testing, one could miss important components of the face recognition impairment or disclose processing differences between the damaged and normal face processing systems that are not central to prosopagnosia. Moreover, by selectively manipulating the type of information that is diagnostic for the task at hand over a number of trials, subjects may be forced to rely on this information (e.g., the mouth) and learn strategies to dramatically improve their performance (Barton, Press, Keenan, & O'Connor, 2002; Barton, Cherkasova, & O'Connor, 2001). Thus, a better approach to determine the information used and not used is to bias as little as possible the tested information. To this end, we trained and tested a single patient (PS) suffering from a remarkably selective deficit at processing faces following brain damage (Rossion et al., 2003) with Bubbles (Gosselin & Schyns, 2001), a low-bias sampling technique that can determine the specific visual information used to categorize a visual stimulus.

PS is a 54-year-old woman who sustained a closed head injury in 1991. After several months of spontaneous recovery and neuropsychological reeducation, she was left with massive prosopagnosia, being unable to recognize famous and familiar people. Despite large occipital and occipitotemporal lesions (see Figure 1 in Rossion et al., 2003), PS's low-level vision is almost perfect, her visual acuity being 8/10 in both eyes (August 2003), with a full visual field, apart from a small left paracentral scotoma. She reads normally (although slowly) and, crucially, does not present any problem at object perception and recognition, even for subordinate-level discriminations (Rossion et al., 2003). Her deficit truly appears to be restricted to the category of faces. With faces, PS is able to categorize a face as a face, discriminate faces from objects and from a complex scene background, even at brief presentations (100 msec; Schiltz et al., in press). Her gender and expression performances are relatively well preserved, although slightly below normal range (Rossion et al., 2003). This is in stark contrast with her inability to recognize previously seen or familiar faces and to match unfamiliar faces (see Methods section). In sum, PS is unable to derive an individual representation of a face that is both selective and invariant (robust) enough so that it can be discriminated from other faces and be associated with the same or other views of the same face (Rossion et al., 2003).

Given the restriction of her deficit to the face category and that PS is alert, cooperative, and without

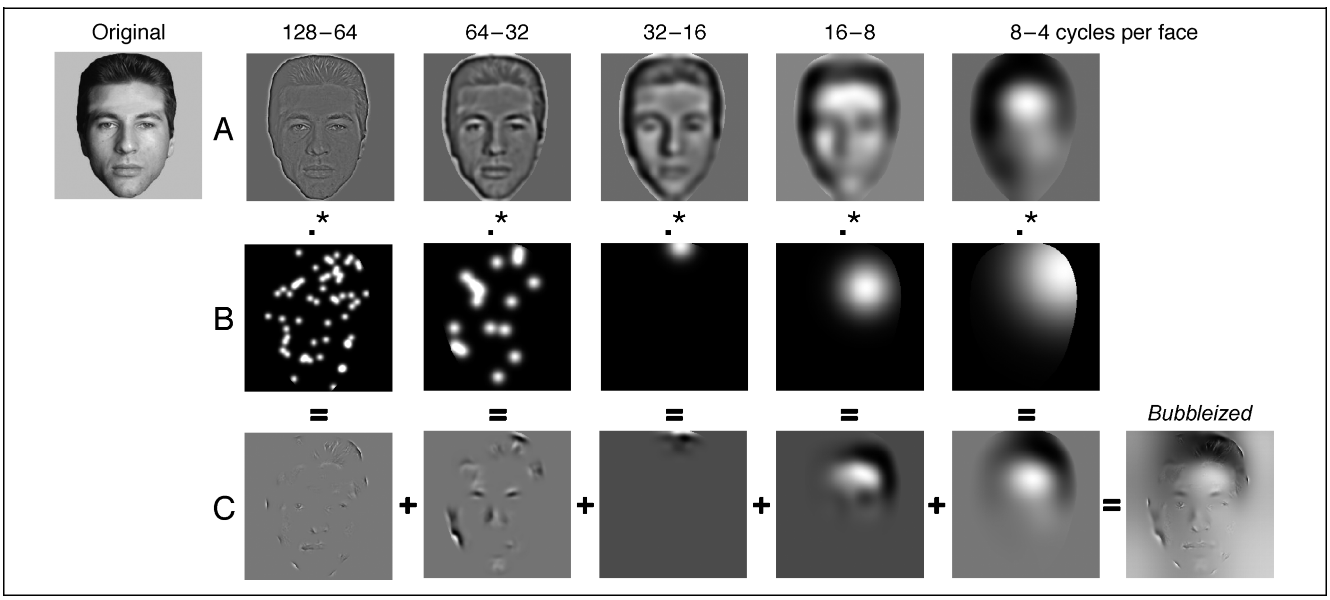

Figure 1. Application of Bubbles technique to the three-dimensional space composed of a two-dimensional face and spatial scales on the third dimension. (A) The original image is decomposed into five different scales. (B) The bubbles were randomly positioned at each scale and covered approximately the same area across scales. (C) The bubbles were integrated with the decomposed pictures and summed to result in a "bubbleized" face.

any learning difficulties (Caldara et al., submitted), she may represent an ideal case to isolate the nature of the facial information extracted by an impaired face processing system, relative to normals. Moreover, although relying also on nonfacial cues to identify faces, PS reports using facial cues in general and does not avoid looking at people's faces. Her performance at matching tasks is under normal range, but generally better than chance (Caldara et al., submitted; Schiltz et al., in press; Rossion et al., 2003). Hence, her face processing system, although inefficient at recognizing individual faces, is not completely disrupted, as supported by the significant face-sensitive activations observed in her right hemisphere in the fusiform gyrus (Rossion et al., 2003) and also in the superior temporal sulcus and the dorsolateral prefrontal cortex (Sorger et al., 2004).

To specify PS's use of facial information, we used Bubbles (Gosselin & Schyns, 2001), a response classification technique sampling the information in 3-D space (2-D image × spatial frequencies). Bubbles samples an input space to present sparse versions of the faces as stimuli (see Figure 1). PS and normal controls must categorize the sparse stimuli, and Bubbles keeps track of the samples of information that lead to correct and incorrect identification responses. From this information, we can establish how each region of the input space contributed to face identification performance and depict the selective use with an *effective stimulus*.

In the present study, we applied this technique to PS and a group of control participants, who identified a set of previously learned unfamiliar faces displaying two possible expressions (neutral or happy) (see Methods) (Schyns et al., 2002).

RESULTS

The proportion of the search space, revealed at each trial, was adjusted on-line to maintain accuracy at 75% correct by adjusting the total number of bubbles sampling the input (see Methods and Gosselin & Schyns, 2001). Following the experiment, independently for each subject and session of trials, we averaged across trials the number of bubbles required to resolve the task.

Overall, PS required many more bubbles (mean = 157; SD = 30) than controls (mean = 38; SD = 17, $Z = 7.04$, $p < .001$; Figure 2), meaning that PS needed more facial cues, on average, to achieve the same performance level. Even her lowest number of bubbles, recorded on her last session (116), was much larger than that of controls (mean = 25; SD = 6; $Z = 14.89$, $p < .001$), even though PS was allowed to perform approximately twice as many trials as the controls (Figure 2, see Methods section). Another striking measure is the proportion of decrease in number of bubbles between the first three and the last three

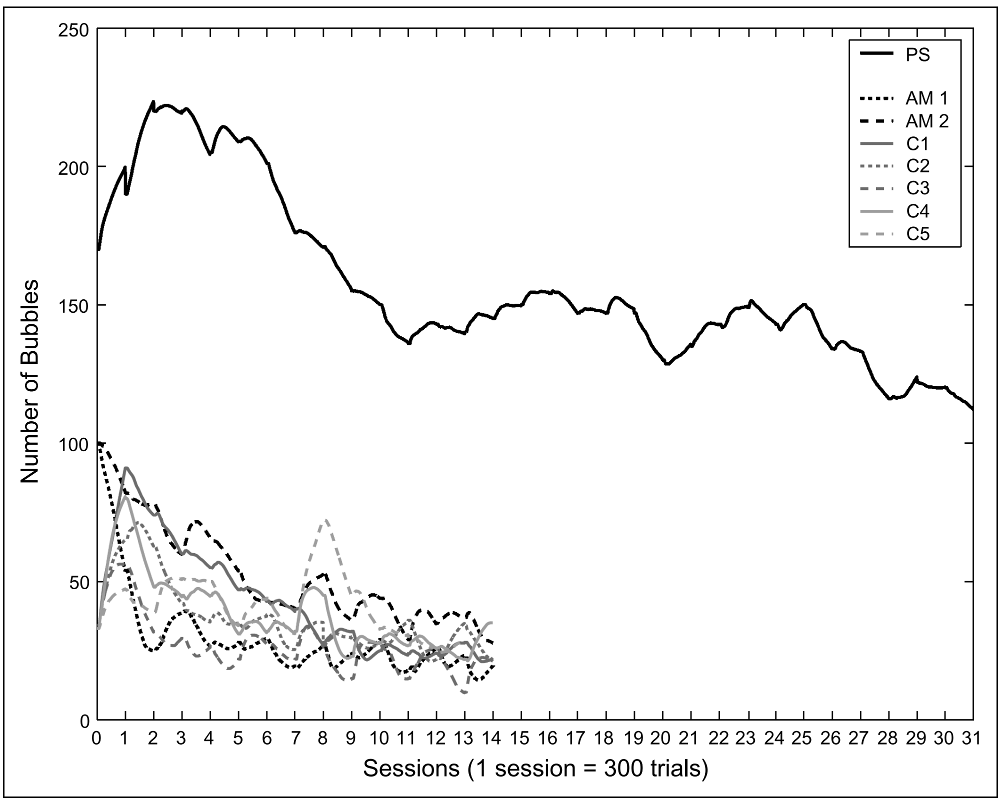

Figure 2. Mean number of bubbles per session used by PS and seven controls to correctly adapt to the task (AM = age-matched controls; C = young adult control subjects). The performance for all the participants was automatically kept to a 75% correct identification.

sessions, which was 54% ($SD = 8\%$) for controls, but only 42% for PS ($Z = -2.16$, $p < .01$).

These descriptive results illustrate not only that the face processing system of PS is not as efficient as that of normal subjects, but also that PS can still extract some diagnostic information to identify faces at 75% correct. To address the critical question of the nature of this diagnostic information, we compared PS's effective stimulus with the average of controls ($p < .05$, see Methods and Figure 3). PS does not use information from the upper part of faces (i.e., the eyes) to identify them, but instead relies mainly on the lower part of faces (i.e., the mouth). In contrast, all controls used the eyes and some of the mouth, with a bias toward the upper part of the face (see also Schyns et al., 2002; Gosselin & Schyns, 2001).

From the diagnostic information, we also compared the relative use of spatial frequency information between PS and controls. To this end, independently for each spatial frequency (SF) band sampled, we pooled the ProportionPlanes of all controls and Z scored them. To evaluate PS's relative use of SF bands in a normative context (the performance context of controls), for each SF bands we averaged PS's Z scores computed using the mean and standard deviation of controls. Figure 4 reveals that PS used the high spatial frequency bands to encode the mouth, in contrast to controls who used significantly more high spatial frequencies to encode the eyes. Finally, we derived a fine-grain, pixel-per-pixel evaluation of PS's use of information in a direct comparison with controls. Independently for each SF band, we took the logarithm of the division of the ProportionPlane of PS with the average ProportionPlane of controls. We then summed these logarithms to derive a measure of sensitivity to information (see Methods and Smith et al., 2005). This measure provides an account of the relative sensitivity of PS to all aspects of the face, on a pixel-per-pixel basis, in the identity task. To read the figure, red (vs. blue) values indicate a higher (vs. lower) sensitivity of PS with respect to controls. The results clearly show that for face identification, PS uses suboptimally the eyes (particularly the left one) and she has a clear bias to the outline contours and the lower part of the face, including the mouth (see Figure 5). To further specify theses biases, we isolated the Z scores over the eyes and the mouth regions for PS and for the average performance of controls. We then built the distributions of Z scores across scales, subtracted the Z scores between controls and PS, and depicted the resulting Z score distributions (Figure 5, right). PS used significantly less the eyes (negative values) than the mouth (positive values) to achieve correct identifications ($Z > 1.65$; $p < .05$). Conversely, controls used less the mouth than the eyes to perform the task efficiently.

DISCUSSION

Our general goal was to shed light on the nature of the missing and preserved components of the face processing system when it is selectively—albeit not entirely—damaged. The first observation was that the prosopagnosic patient PS and controls dramatically differed in the amount of information needed (i.e., number of bubbles) to recognize an individual face. Furthermore, PS improved throughout the recognition sessions, using progressively less information. Her ''learning curve'' was, however, less steep than normal controls, including age-matched subjects. Of particular interest, PS and controls differed on the type of information used to recognize faces. PS relied much less on information contained in the upper part of the face (the eye

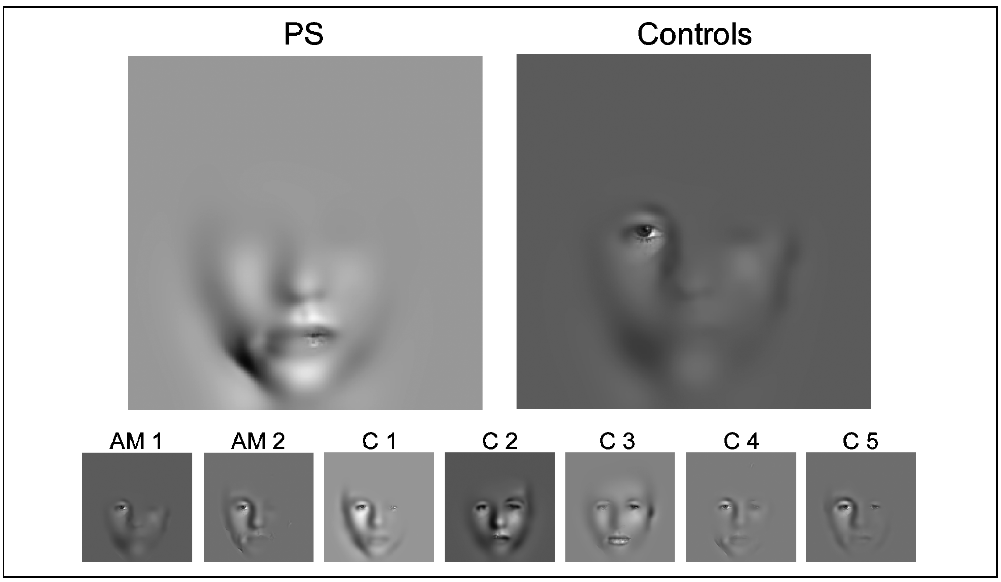

Figure 3. Top: diagnostic information used by PS and the average for the controls. Bottom: diagnostic information for each control subject (AM = age-matched; C = young adult control subjects). Note that PS is the only participant that did not use the eyes to adapt to the task.

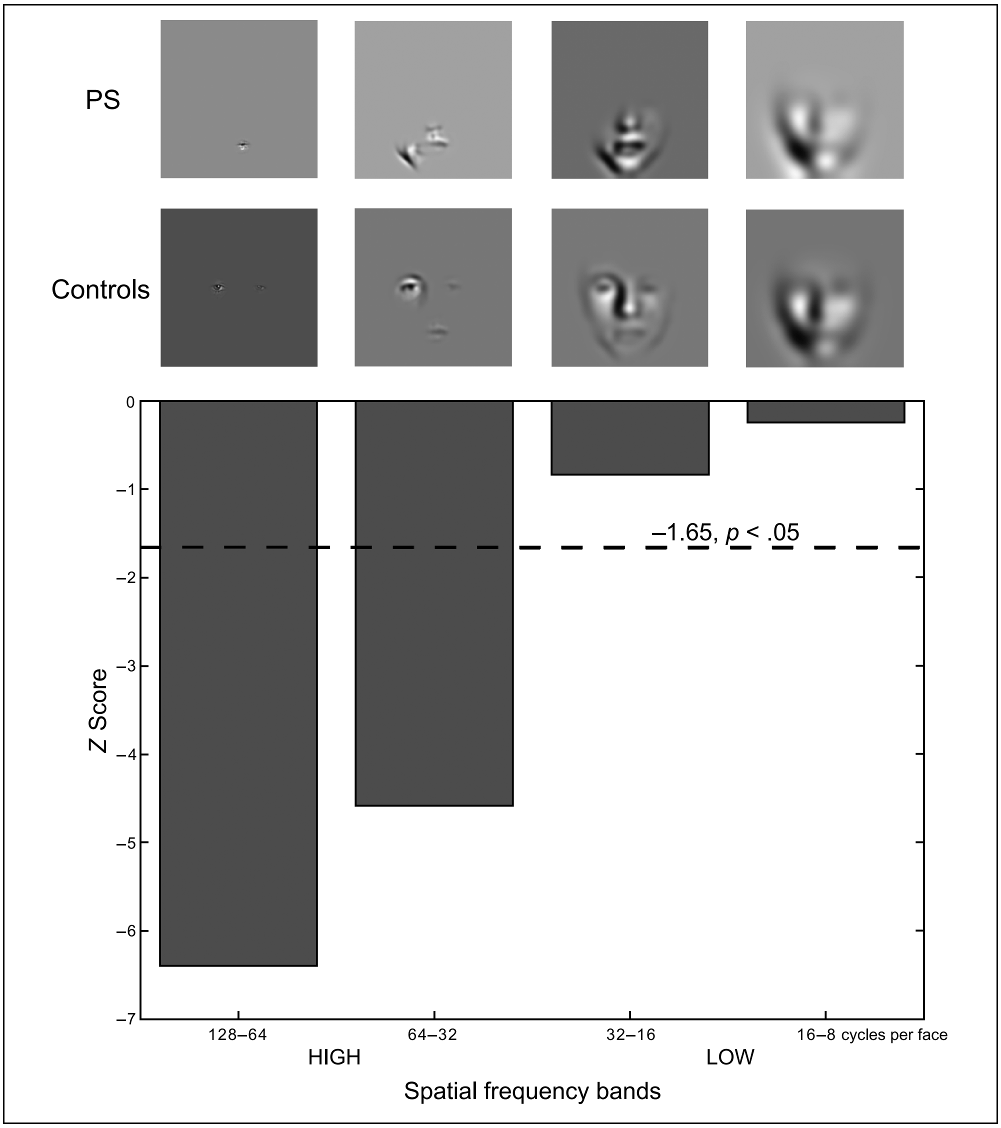

Figure 4. Top and middle: diagnostic information used to resolve the identification task at each independent scale for PS and the controls. Note that three control subjects did not use any significant information for the scale going from 16 to 8 cycles per face. Bottom: patient PS's Z score distributions in the use of spatial frequency bands. The dashed line indicates a Z score of -1.65 ($p < .05$). PS used significantly less high spatial frequency information (128–64 and 64–32 cycles per face) when compared to the control group. Note that no meaningful information was found at the fifth frequency (coarsest scale) for PS or the controls.

region), but in stark contrast with controls, she used the lower part, particularly the mouth. She also presented a bias to use of the outline contour of the faces. Finally, PS was more impaired in extracting information in high spatial frequencies, but did not differ from normals for low spatial frequency bands. We discuss these findings in turn.

Quantitative Assessment of Visual Information

The observation that PS required *a larger number of bubbles* than normal controls can be considered as another illustration of her dramatic face processing impairment. In previous behavioral experiments, she was less accurate and/or slower when having to discriminate and recognize faces at the individual level (Rossion et al., 2003). Remember that PS was extensively trained with full-face stimuli before the Bubbles sessions to reach the same level of faultless performance as controls. In the present study, her recognition performance with faces revealed through the Bubbles apertures was maintained at the same threshold as normals (75%) throughout the whole experiment. In other words, she required *more* information to reach the *same* level of performance as controls. Whereas normal observers can extract information from a relatively degraded image to match their internal representation of a given face, she needed more information. This result cannot be accounted for by a general learning problem (face–name associations) because PS has no known learning or memory deficits (Mayer, Fistarol, & Valenza, 1999). In fact, she can name common objects normally and even learn arbitrary associations between shapes and names rapidly (Rossion et al., 2003).

Although the fact that a prosopagnosic can learn and recognize 10 face–name associations might be paradoxical at first glance, one must point out that she needed 3 hr to be flawless, whereas controls achieved this

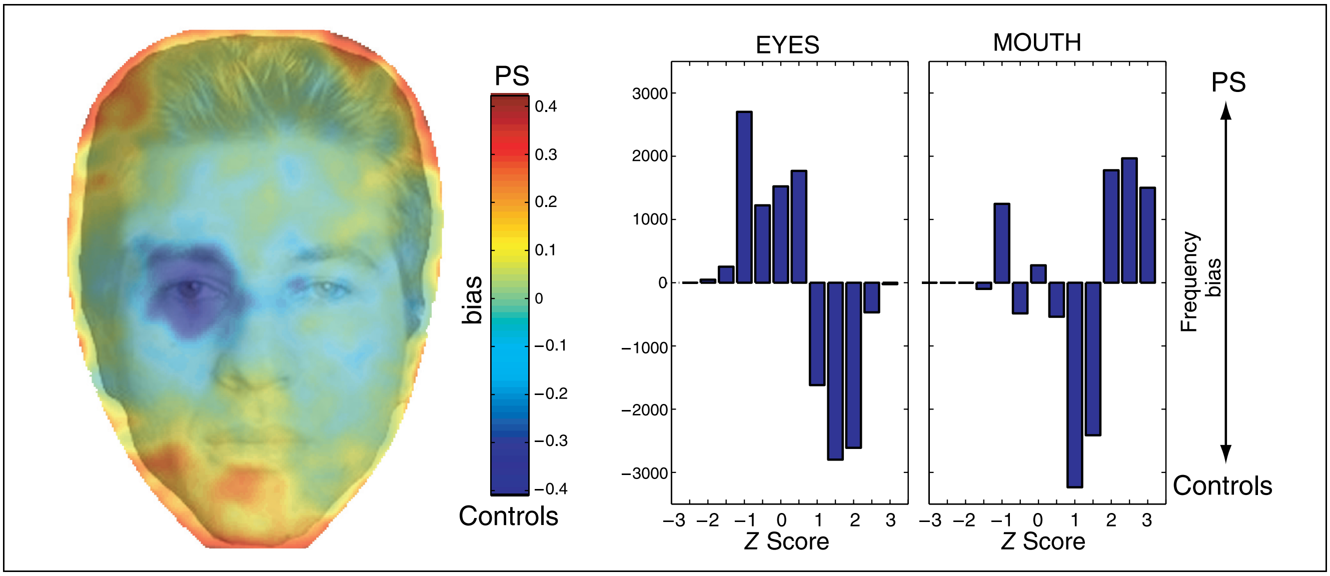

Figure 5. Left: optimality of the information used by PS compared to the control group. Dark blue regions correspond to negative values and illustrate a suboptimal use of information. Light blue regions correspond to values close to 0, a comparable use of information. The red and yellow areas correspond to positive values, reflecting the bias of PS in the task. Right: distribution of the performances in the Eyes and Mouth regions, after the subtraction of PS's Z score distributions from the controls. Z scores >1.65 indicates when these particular features were significantly ($p < .05$) used as diagnostic information. A positive value indicates a bias for PS; a negative value indicates a bias for the controls. Note that PS was more efficient for the Mouth ($Z > 1.65$; $p < .05$) than the Eyes region. The reverse pattern is observed for the controls.

ceiling performance in about 10 min. Furthermore, previous studies of prosopagnosic patients have reported that they are able to learn up to 12 new face–name associations, and retrieve them consciously (Sergent & Signoret, 1992; Dixon, Bub, & Arguin, 1998) or unconsciously (de Haan, Young, & Newcombe, 1987; Bruyer et al., 1983), although this learning is slow and does not generalize well to new views (e.g., three quarters to full front and vice versa) of the same faces (Sergent & Signoret, 1992). Even when the exact same picture is used for learning and testing, prosopagnosic patients usually perform well below normal range (Sergent & Signoret, 1992).

Given that she had as much time as she wished during the recognition tests with Bubbles, the observation that she needed more information in the degraded (''bubbleized'') faces to recover the facial attributes necessary to match against her stored representations suggests that these are poorer than in normals. This observation does not necessarily mean that PS's prosopagnosia lies in the associative level and that her perception of faces is normal (i.e., a ''pure associative prosopagnosia''). In fact, her inability to match normal face pictures presented under identical or different viewpoints and the locus of her lesions (Schiltz et al., in press; Rossion et al., 2003) point to a face deficit of high level visual processes. However, as pointed out previously, disruption at the perceptual level of the face processing system may disable a set of face processes, making it impossible to encode rich facial representations in memory (Sergent & Signoret, 1992; Farah, 1990).

Qualitative Assessment of Visual Information

In what respects then, are PS's internal representations of faces poorer than normals? Behavioral and neurophysiological evidence suggest that faces are represented both in terms of individual features (e.g., eyes, nose, mouth, etc.) and also as undissociated wholes (Tanaka & Farah, 1993; Perrett, Hietanen, Oram, & Benson, 1992; Perrett, Rolls, & Caan, 1982). Behavioral studies have also pointed to the importance of the metric distances between face features (e.g., between eyes and nose), the so-called second-order relations (Diamond & Carey, 1986), to recognize faces (for a review on the different types of configural processing, see Maurer, Grand, & Mondloch, 2002). In the present experiment, it may well be that normal controls require less information than PS because their internal representations are more detailed at the level of critical single features such as the eyes. Alternatively, normal controls' featural representations may be better integrated into holistic facial templates (Tanaka & Farah, 1993), allowing one to reconstruct full facial representations from smaller fragments of the face than PS. An analysis of the *quality* of PS's internal representation of the faces, that is, which parts of the face are and/or are not represented, may help to clarify this question.

A striking feature of PS's diagnostic information is that it is weighted less on the upper part of the face (eyes/eyebrows) than on the lower part (mouth area). Admittedly, the dominant reliance of PS on the mouth area may not hold for all the faces of the set,[1] and there is a certain amount of interindividual variability for the average diagnostic image in normal controls (Figure 3). Yet, the general pattern of respective diagnostic facial information observed is clear: Whereas the region of the eyes dominated the picture for normal subjects, PS weighted strongly the area around the mouth of the face. This finding suggests that PS's internal representations of the faces contain mostly information in the mouth area, whereas the normal face processing system relies largely on the eyes (see also Schyns et al., 2002; Gosselin & Schyns, 2001).

There is considerable evidence supporting the view that the eyes are dominant in the recognition of facial identity. Human adults can recognize and remember faces from the eyes only (McKelvie, 1976) and experiments designed to measure the relative importance of different facial features for individual face recognition have consistently shown the dominance of the eye/eyebrow combination, followed by the mouth and then the nose (Tanaka & Farah, 1993; Fraser, Craig, & Parker, 1990; Haig, 1985, 1986; Sergent, 1984; Walker Smith, 1978; Davies, Ellis, & Shepherd, 1977). In fact, recent evidence even suggests that the eyebrows alone convey critical information to recognize faces (Sekuler et al., 2004; Vinette, Gosselin, & Schyns, 2004; Sadr, Jarudi, & Sinha, 2003).

Given these considerations, there are several possible explanations regarding the decreased reliance on the eyes area following prosopagnosia, as found in PS.

First, given that the eye area contains more information in high spatial frequencies (HSFs), it may be thought that PS's lesser reliance on the eyes reflects a general deficit with HSFs. This observation would be in agreement with previous reports of reduced contrast sensitivity in the high-frequency range for nonfacial stimuli in prosopagnosic patients (Barton, Cherkasova, Press, Intriligator, & O'Connor, 2004; Rizzo, Corbett, Thompson, & Damasio, 1986), although there are reports of prosopagnosic patients having a marked deficit at resolving mostly low spatial frequencies on face stimuli (e.g., Sergent & Villemure, 1989). Critically, in the present experiment there is clear evidence that PS uses HSFs for the mouth and that the deficit is not related to HSF processing per se, but to the encoding of information from the eyes, at any SF.

Second, following her brain damage, PS may have lost the ability to extract other information than the cues associated with identity on the eye region (e.g., expression, eye-gaze direction) and would have turned her interest to different (e.g., the mouth) face cues when interacting with others. However, whereas she reports being unable to recognize people, she does not complain at all about judging people's expressions, and her ability to categorize facial expressions on pictures is relatively preserved as compared to identity (Rossion et al., 2003). There is no evidence either that she lost her ability to detect eye gaze direction, although this has not been tested previously. Furthermore, PS's lesions spare entirely the region of the posterior superior temporal sulcus responding to faces (Sorger et al., 2004), which subtends eye-gaze detection in normals (Hoffman & Haxby, 2000). These behavioral and anatomical observations suggest that her deficit in processing the eye region is unlikely to be explained by a general impairment in extracting social cues from the eyes.

A third hypothesis that may account for PS's decrease in the representation of the eyes is also indirect. Given her inability to recognize faces, she may have developed some strategies over time to be able to recognize people while avoiding the embarrassment caused by staring. Indeed, it is well known that prosopagnosics report avoiding looking at people they encounter in the eyes because they need quite some time and numerous cues to recognize familiar persons and one cannot afford staring at people for long periods (Gauthier et al., 1999). According to these views, PS might have overrepresented the mouth area for reasons that have nothing to do with the structure of the face and the loss of her face individual recognition abilities per se, but as a result of the development of new strategies following her impairment. However, as far as we can tell from interactions with her and from her verbal reports, she does not avoid eye-to-eye contact in real-life situations. As a matter of fact, she is a very lively and "social" person, who—as with other prosopagnosics—has developed a number of strategies to cope positively with her deficit in real-life situations: Rather than avoiding people, she will try to anticipate and rely on all possible cues (facial and nonfacial) to be able to recognize them efficiently and rapidly, but then will engage in normal social interactions with these persons. During the experiment, PS verbally reported information on all face features (eyes, eyebrows, teeth, etc.). She often described the presented face before giving an answer, suggesting that she explored the entire image. Moreover, PS's highest reliance on the mouth and on external facial features relative to normals concurs with her verbal reports about people she encountered after her accident. When asked about how people she met in the laboratory look like, for instance, she always refers to the shape of the mouth and teeth area, as well as to external contour information (hair, head size, etc.).

Although the last two hypotheses cannot be completely dismissed, we favor the hypothesis that her overrepresentation of the mouth area at the expense of the eyes has to do with the interaction between the structure of the faces—what type of cues are conveyed by the eyes—and the expertise of the face processing system with these cues. Several observations support this hypothesis. When presented in isolation, the eye area can be conceived as a visual structure made up of several (pairs of) components (i.e., eyebrows, eyelid, eyelash, eyeball, pupil, and iris). As such, there is much configural information (e.g., distance between the eyes, between the eyebrows and the eyes) in this structure, much more so than in other internal facial features such as the mouth and the nose, as demonstrated in several experiments by Leder, Candrian, Huber, and Bruce (2001) and Leder and Bruce (2000). These authors showed that configural information is not limited to the whole face but consist at least partly of locally processed relations between facial elements, in particular at the level of the eyes. Rakover and Teucher (1997) also found inversion effects for isolated features and showed larger effects for the eye area than for the mouth, suggesting that the former conveys more configural information. In fact, a large number of studies showing the important role of configural information in face perception mostly or exclusively used spatial changes (e.g., inward/outward or up/down movements) at the level of the eyes (e.g., Leder et al., 2001; Macho & Leder, 1998; Kemp, McManus, & Pigott, 1990; Hosie, Ellis, & Haig, 1988; Haig, 1984). Corroborating yet again the critical role of the eye region in supporting configural information, there is evidence from the whole/part advantage paradigm that the holistic processing of the face is larger for the eyes than for other features (Donnelly & Davidoff, 1999). Most interestingly, whereas the whole/part advantage is observed for the mouth on unfamiliar faces and does not increase with familiarization, this effect appears only for the eyes after substantial training with a face set (Donnelly & Davidoff, 1999). Thus, the ability to extract and use configural information on the eyes seems to develop over time and concerns mostly familiar faces. This is also the conclusion of two experiments conducted by O'Donnell and Bruce (2001), which tested subjects' discrimination abilities on pairs of familiar and unfamiliar faces with subtle differences at the level of one of four features (hair, jaw, eye, and mouth). Strikingly, when faces differed only by the eyes, the subjects' performance was excellent for familiar faces (above 90%) and below chance for unfamiliar faces. There was no effect of familiarity for the other features, including the mouth. This familiarity effect restricted to the eyes was found whether the modifications were configural (eye spacing, Experiment 1) or local (brightness change, Experiment 2). The conclusion of the authors is that details from the upper part of the face may offer particularly salient information in the initial structuring of categorical knowledge about individual faces (O'Donnell & Bruce, 2001). This holds obviously for a normally functioning face processing system. The present study, contrasting the representations used by normal viewers and a damaged face processing system, indicates that a critical feature of prosopagnosia is the inability to extract such salient information, largely conveyed by the eye area, to build robust representations of faces.

To sum up, we suggest that relative to normals, PS does not rely on eyes because her face processing system is not able to extract and store information, perhaps mostly configural, from this area of the face. One difficulty with this version of Bubbles is that the features of the different faces were presented at the same locations across the different faces of the set (Gosselin & Schyns, 2001), minimizing the diagnosticity of configural metric information (Maurer et al., 2002; Diamond & Carey, 1986) to individualize faces. However, by revealing the face features used by the subjects, for instance, the eyes, the nose, and the mouth for a face identification task, Bubbles can reveal the use of the face features that are essential for proper configural processing. The absence of the use of the eyes in patient PS reflects an inability to extract information that is known to be critical for configural processing of faces in normal viewers, although we cannot exclude at this stage that PS suffers mainly from a deficit at extracting both configural and local information in this area of the face.

Besides a suboptimal use of the eye region, PS relied much less on internal features than on external features (i.e., contour), relative to normals (Figure 5, left). This observation can also be related to the inner-features advantage observed for familiar faces in normals, namely, the robust finding that the inner-face parts are more useful than those of the outer face for recognizing familiar faces but not unfamiliar faces (Campbell, Coleman, et al., 1999; Young et al., 1986; Ellis, Shepherd, & Davies, 1979). Because this inner-features advantage is found only with familiar faces, it is associated with the ''memorial representation of the known individual'' (Campbell, Coleman, et al., 1999). When encoding faces in memory, the normal face processing system appears to give more weight to internal face features. In contrast, our data show that although PS managed to encode faces in memory, she relied less than controls on inner facial features, similarly to her lesser reliance on the eye area of the face. To our knowledge, the inner-face advantage for familiar faces has not been tested in prosopagnosics previously, given their difficulties in recognizing faces. However, a normal inner-face advantage was found in posterior left- and right-brain-damaged patients without prosopagnosia (de Haan & Hay, 1986), suggesting that the lesser reliance on internal features of faces observed in patient PS may be specific to the prosopagnosic deficit.

The literature covered above suggests that both the reliance on facial configuration, particularly at the level of the eyes, and the advantage given to internal features reflect important characteristics of the normal adult face processing system, allowing the recognition of individual familiar faces. Quite interestingly, these features of the face processing system appear to undergo a long developmental course, relative to other aspects of face processing. The inner-face advantage for familiar faces, for instance, is found only at 15 years old, children before that age showing an outer-face advantage (Campbell, Coleman, et al., 1999; see also Carey & Diamond, 1977). Other evidence suggests that although the early months of visual experience may be critical for the normal development of facial configuration processes (Le Grand, Mondloch, Maurer, & Brent, 2001, 2004), this ability develops relatively slowly compared to the capacity to extract individual features (Mondloch, Le Grand, & Maurer, 2002) and may not be achieved fully until mid-adolescence (Carey & Diamond, 1994; Ellis & Ellis, 1994; Carey, 1992).

Considering together the literature and the data reported here, we suggest that the fundamental properties of the face processing system that undergo a long developmental course may also be the most sensitive—that is, the first to be disrupted—when selective damage occurs to this system. Admittedly, this suggestion needs complementary evidence, such as showing how PS deals with various face information on ''familiar'' and unfamiliar faces relative to normals in simple discrimination tasks, for instance. Most importantly, it remains to be seen whether other cases of prosopagnosia with at least relatively well-preserved non-face recognition processes, show the lesser reliance on the eyes area and internal face features in general. As stated in the Introduction, there is considerable variability between acquired prosopagnosics with respect to lesion localization and extent, performance on various discrimination and recognition tasks, and strategies used to compensate for their deficit (e.g., Sergent & Signoret, 1992). Yet, common patterns of functional impairments can also be found in such cases despite different lesion localizations, for instance (e.g., Barton, Press, et al., 2002; Damasio et al., 1982). The investigation reported here is made on a single case and will need complementary evidence from other patients to be recognized as a key feature of acquired prosopagnosia. However, if we are correct about the reasons why PS shows a lesser reliance on the eyes and internal region of the face, we expect to find such a pattern of performance in other acquired cases of prosopagnosia, provided that they have preserved low-level vision and long-term visual memory, allowing them to extract and store diagnostic information from isolated face cues. Recent investigations using simultaneous discrimination tasks with full face stimuli on patient LR, a case of prosopagnosia following a lesion in the anterior part of the right temporal lobe, support this view, showing that he relies mostly on the mouth area (Bukach, Bub, Gauthier, & Tarr, in press). Interestingly, this patient also presents a deficit restricted to faces and a remarkably preserved low-level vision. Finally, future studies will also have to determine whether the present findings can be generalized to cases of congenital prosopagnosia (CP), the lifelong impairment in face processing that is apparent from birth (for a review, see Kress & Daum, 2003). Despite an increasing interest in CP in the last couple of years, many findings remain inconsistent, but recent careful investigations of a group of congenital prosopagnosics suggest that such patients have deficits that are not limited to faces and may be due to a general inability to derive a global configuration from local elements (Behrmann, Avidan, Marotta, & Kimchi, 2005). These CP patients have never developed an expertise at processing faces and thus will probably have qualitatively different ''facial representations'' than cases of acquired prosopagnosia, a topic of interest for future studies.

Conclusions

Testing a single case of acquired prosopagnosia with Bubbles gives clues about how faces can be represented by a selectively disrupted face processing system relative to normals. The data collected show that PS's internal representations of ''familiar'' faces is less robust and specific than in normals, requiring more information from the percept to be activated and discriminated from other representations. Qualitatively, PS's representations appear to be weighted less toward the eyes and the internal features in general, which are critical components of a normal adult face processing system having to build and store robust representations of individual faces. Finally, in the framework of high-level visual neuropsychological diseases, the Bubbles technique might represent a promising instrument for identifying in the patients the preserved visual representations and, as a consequence, exploiting this information for their rehabilitation.

METHODS

Subjects

Case Report

PS is a case of acquired prosopagnosia with normal object recognition who has been reported in detail elsewhere (Rossion et al., 2003) and will be only briefly described here. She is a 53-year-old woman (born in 1950) who sustained a closed head injury in 1992, causing lesions of the lateral part of the occipital and temporal lobes, bilaterally (see Figure 1 in Rossion et al., 2003). Despite the extent of the lesions in the visual system, PS has normal low-level visual processing. PS is ranked as highly impaired on the Benton Face Matching Test (Benton & van Allen, 1972), scoring 27/54 (percentile 1). She is also impaired on the Short Recognition Memory Test for Faces, a set of the Camden Memory Tests (Warrington, 1984, 1996), scoring 18/25 (percentile 3). Regarding the recognition of familiar faces, when PS was confronted with the pictures of 60 famous people (all known by the patient), she was able to classify 14 of them as familiar, and correctly classified all the unfamiliar ones. Nevertheless, when she had to report the individual names of the faces classified as familiar, as well as their associated semantic information, drastically, she was correct for only four of them. Although much better than controls for individual discrimination, PS is not as good as controls at gender and facial expression judgments but has normal performances of age assessment on faces (Rossion et al., 2003). She is also able to draw correctly a schematic face and perfectly point out all the single features. Finally, PS has been tested extensively with simultaneous and delayed face and nonface (cars and novel objects) matching tasks in previous studies (Rossion et al., 2003). Although she is consistently dramatically impaired and slowed down for the face conditions, her performance with the nonface objects is in the normal range.

Controls

Five young adults (mean age, 27) and two age- and education-level-matched controls (one woman and one man, ages 54 and 57 years, respectively) voluntarily participated in the experiment. All the subjects were healthy and had no neurological or psychiatric history.

Stimuli

Ten unfamiliar faces (5 women, 5 men) displaying two possible expressions (neutral or happy) were used in the experiment. All faces had a normalized hairstyle, global orientation, and lighting (Schyns & Oliva, 1999). Bubbles (Gosselin & Schyns, 2001) was applied to generate the stimuli (see Gosselin & Schyns, 2001, for details). Each face is first decomposed into six nonoverlapping bands of spatial frequencies of one octave each. The cutoffs of these bands were, respectively, 90, 45, 22.5, 11.25, 5.62, and 2.81 cycles per face, from the finest to the coarsest scale. The coarsest band was a constant background and is not illustrated in Figure 1. For each spatial frequency band, a number of randomly located Gaussian apertures (called Bubbles) sampled facial information independently at each scale to create a sparse stimulus, that is, a subset of the original facial information. With sufficiently many trials, this technique ensures that the entire face is sampled in the considered spatial frequency bandwidths, that is, Bubbles is an asymptomatically exhaustive, nonbiased sampling.

Procedure

Prior to the Bubbles experiment, all participants received a printed version of all faces and learned them at the individual level (i.e., their names). In a computer-verification task that assessed performances, participants were confronted with each face and instructed to name them by pressing the corresponding computer keyboard key. Feedback displaying the correct name informed subjects of their mistakes. This training procedure ended when subjects performed a perfect identification of all the faces twice in a row. On average, for the controls, only 10 min were sufficient to reach this level and start the experiment. The same procedure was used with the patient PS. However, for her, a 3-hr training program split into 2 days was necessary to achieve this level of face identification. In addition, PS performed this verification procedure before starting each of the Bubbles sessions and had to succeed twice in a row before starting a Bubbles session.

The experiment ran on a Macintosh PowerBook G3 computer using a program written with the Psychophysics (Brainard, 1997; Pelli, 1997) and Pyramid (Simoncelli, 1997) Toolboxes for Matlab and consisted of sessions of 300 trials, randomly presenting 30 times the same identity (10 neutral, 10 happy). All trials were taken into account for the analysis. In each trial, a sparse face appeared on the screen, and the participants had to determine its identity by pressing the corresponding computer keyboard key. The image remained on the screen until the subject responded, and no feedback was provided. Note that PS and the controls were not required to answer as fast as possible, and thus were free to finely examine each stimulus. The number of bubbles was automatically adjusted to maintain subjects' performance at 75% correct. PS performed a total of 9300 experimental trials divided into 31 sessions of 300 trials, spanned over 16 weeks. Controls performed 4200 trials divided into 14 sessions within 3 weeks. PS was tested for twice the number of sessions of the controls for several reasons. First, the number of bubbles for PS over the early sessions was less stable than for controls, and there was an indication that it could still decrease with additional sessions in her case. For instance, PS's number of Bubbles first increased, then decreased and was as large after seven sessions than at the beginning, and then decreased again up to the 12th session. However, the decrease in number of Bubbles took place after two sessions for controls to reach a plateau after seven sessions (Figure 2). This parameter influences the quality of the statistical solutions found by Bubbles, and thus we chose to conduct more sessions with PS until we obtained a stable pattern of performance in terms of number of bubbles. Second, we expected to observe a reduction of the amount of information needed by PS over the extra Bubbles session to get a fine-grained picture of the diagnostic information for her. Finally, although PS agreed to do that many sessions, totaling 9300 trials, allowing us to get a refined picture of the diagnostic facial information for her, there was no need to run controls over 14 sessions, which was enough to characterize their pattern of diagnostic information.

Data Analysis

We hypothesize that on any given trial, if the participant could correctly categorize the sparse face on the basis of the information revealed by the bubbles, that information was sufficient for that face identification. Across trials, we therefore kept track of the locations of the bubbles leading to correct identification for each participant. To this end, for each scale we added the masks with the bubbles leading to correct identifications to create a CorrectPlane [henceforth, CorrectPlane(scale)], where scale information is represented from 1 to 5, from fine to coarse (see Figure 1 for examples of masks). CorrectPlane(scale) therefore encapsulates the locations at each scale where sampling of face information (bubbles) led to correct identifications. We also added the masks with bubbles leading to both correct and incorrect identifications to create TotalPlane(scale). Thus, TotalPlane(scale) represents, for each scale, the total sampling frequency of face information. From the information in CorrectPlane(scale) and TotalPlane(scale), we determined, for each subject separately and on a cell-by-cell basis, the ratio of the number of times a specific location led to a successful face identification over the number of times this location was presented, CorrectPlane(scale)/TotalPlane(scale). We refer to this ratio as ProportionPlane(scale). Across subjects, the averaged ProportionPlane(scale) weighs the importance of the regions of each scale for the identification task. If all regions were equally important, ProportionPlane(scale) would be uniform across cells, and equal to the performance criterion—here, .75. Consequently, regions significantly above (vs. below) the performance criterion are more (vs. less) diagnostic. To determine this significance, we built a confidence interval ($p < .05$) around the mean of the ProportionPlane(scale), for each proportion. DiagnosticPlane(scale) was created by representing diagnostic (significant) proportions with a filtering weight of 1 and nondiagnostic proportions with a filtering weight of 0. These diagnostic weights were then used to filter the original stimulus to derive the effective stimulus (see Figure 3), which depicts the selective use of information in the task. The effective stimulus is simply obtained by multiplying the face information at each scale in Figure 1 with the corresponding DiagnosticPlane(scale) convolved with bubbles of the size used during the experiment. The importance of the information used at each spatial frequency bands was compared between PS and the control group (see Figure 4) by normalizing patient PS's results with those of the control group and selecting a confidence interval ($p < .05$) around the mean.

The logarithm of a pixelwise division of the ProportionPlane of patient PS with the averaged ProportionPlane of the control group was computed to determine the optimality/efficiency of information use by the patient compared to the control group (e.g., Smith et al., 2005). Negative and positive values are related to a suboptimal and an optimal processing, respectively, of patient PS (Figure 5, left). The 0 value represents a comparable performance between patient PS and the control group. Finally, to reveal the quality of the performances for the eyes and the mouth facial features, two separate masks covering these face regions were applied to the ProportionPlane of PS and the controls, disclosing the respective distributions for both face features and groups. Then, PS's distributions were subtracted from the controls' distributions for each respective face region, revealing a frequency bias for each facial feature in both populations (Figure 5, right). A positive value in Z score distributions indicates that PS's performances, compared with the controls, occurred more frequently for a particular Z score bin ($Z > 1.65$; $p < .05$). Conversely, a negative value indicates a bias for the control group.

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Notes

1. Although Bubbles would in principle allow an analysis of diagnostic features per face, the number of trials per face would be prohibitively larger (with a patient) to reach statistical significance.

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