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Perception of eye gaze direction in a case of acquired prosopagnosia

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The ability to perceive the direction of eye gaze is critical in social settings. Brain lesions in the superior temporal sulcus (STS) impair this ability. We investigated the perception of gaze direction of PS, a patient suffering from acquired prosopagnosia (Rossion et al., 2003). Despite lesions in the face network, the STS was spared in PS. We assessed perception of gaze direction in PS with upright, inverted, and contrast-reversed faces. Compared to the performance of 11 healthy women matched for age and education, PS demonstrated abnormal discrimination of gaze direction with upright and contrast-reversed faces, but not with inverted faces. Our findings suggest that the inability of the patient to process faces holistically weakened her perception of gaze direction, especially in demanding tasks.

Keywords: prosopagnosia, gaze, gaze direction, face perception, social attention

La capacité de percevoir la direction du regard est essentielle dans les contextes sociaux, mais peut être altérée par les lésions cérébrales dans le sillon temporal supérieur (STS). Nous avons étudié la perception du regard dans un cas pur de prosopagnosie acquise, la patiente PS (Rossion et al., 2003). Malgré des lésions dans le réseau cérébral traitant les visages, le STS a été épargné chez PS. Nous avons évalué la perception de la direction du regard en présentant des visages droits, inversés et avec contraste inversé. En comparaison à 11 femmes saines appariées en âge et éducation, les performances de la patiente ont montré une discrimination anormale du regard uniquement avec les visages droits et à contraste inversé. Nos résultats suggèrent que l'incapacité de la patiente à traiter des visages de manière holistique a réduit sa capacité à percevoir la direction du regard, en particulier quand la tâche est exigeante.

Mots clés : prosopagnosie, regard, direction du regard, perception du visage, attention sociale

The human face is the principal cue to recognize people we know. However, faces convey more than information about identity. Other social information such as emotions or intentions might be inferred by diagnostic facial features. Specifically, intentions can be inferred from head orientation or gaze direction (Allison, Puce, & McCarthy, 2000; Nummenmaa & Calder, 2009). In addition, gaze direction indicates another person's focus of attention and allows for gaze following in joint attention (Emery, 2000). Thus, perception of gaze provides humans with critical information for day-to-day social interaction.

Distinct mechanisms and neural substrates underlie the ability to recognize faces and gaze direction. In 1986, Bruce and Young proposed a cognitive model in which two distinct mechanisms enable the visual analysis of a face. One mechanism would process the invariant aspects of a face (i.e., identity), while another mechanism would process the changing aspects of a face (i.e., facial expressions, or movements of mouth and lips). Consequently, facial expressions and gaze direction would be processed by brain networks independent of those responsible for face recognition. Accordingly, neuroimaging studies confirmed specialized neural processing systems that are specific to invariant and changing aspects of a face (see Haxby, Hoffman, & Gobbini, 2000). Two brain regions have been shown to contribute to the processing of invariant aspects of the face: the fusiform face area (FFA) and the occipital face area (OFA). The FFA is a module specific to holistic face processing (Kanwisher, McDermott, & Chun, 1997; Rossion et al., 2000). The OFA, situated in the inferior occipital cortex posterior to the FFA, is also more sensitive to faces than non-face objects (Gauthier et al., 2000; Rossion et al., 2000). Activity in the OFA reflects processing of internal and external facial features, like eyes, nose and hair (Kamps, Morris, & Dilks, 2019). Haxby et al. (2000) suggested that the FFA receives information about facial features from the OFA. Further, the recognition of facial identity is achieved through a holistic or configural process in

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which the different parts of the face are simultaneously integrated into a single representation rather than being processed separately (Bruce & Humphreys, 1994). To date, however, none of these brain regions is considered critical in the perception of gaze direction.

The perception of gaze direction is associated with a brain network that involves the posterior superior temporal sulcus (posterior STS) (Hoffman & Haxby, 2000). Many studies support the critical contribution of the STS in analyzing the direction of gaze in humans (Allison et al., 2000; Calder et al., 2007; Carlin, Calder, Kriegeskorte, Nili, & Rowe, 2011; Ethofer, Gschwind, & Vuilleumier, 2011; Haxby et al., 2000; Hoffman & Haxby, 2000; Nummenmaa & Calder 2009; Puce, Allison, Bentin, Gore, & McCarthy, 1998; Wicker, Michel, Henaff, & Decety 1998) and in non-human primates (Perrett, Rolls, & Caan, 1982; Perrett et al., 1985).

In addition to neuroimaging and animal studies, insights into the distinct neural networks for the processing of invariant and changing features of faces come from the observation of patients with focal brain lesions. These lesions lead to a selective deficit in the ability to recognize familiar faces (e.g., family, relatives, friends, famous people), but a relatively preserved capacity to recognize objects. The condition is referred to as prosopagnosia (Hecaen & Angelergues, 1962; McNeil & Warrington, 1993). Typically, prosopagnosia is associated with right hemispheric lesions in the ventral occipito-temporal cortex (De Renzi, 1986), which is where the occipital and fusiform face areas (FFA) are located (Benton, 1980; Damasio, Damasio, & Van Hoesen, 1982). Prosopagnosia is a very rare condition that cannot be explained by low-level visual deficits or by cognitive impairment (e.g., confusion, aphasia, amnesia, or other forms of intellectual deterioration; Joubert, Rossion, & Busigny, 2008). Interestingly, patients suffering from prosopagnosia are often able to judge the gender, the age and the dynamic aspects of a face (Sergent & Poncet, 1990; Tranel, Damasio, & Damasio, 1988). For instance, the ability to determine gaze direction of frontal faces was preserved in seven cases of prosopagnosia (Duchaine, Jenkins, Germine, & Calder, 2009) and the capacity to accurately judge gaze direction was preserved in one case of acquired prosopagnosia, the patient PS (Burra, Kerzel, & Ramon, 2017).

Conversely, lesions of the STS impair gaze perception in humans and non-human primates. In macaques, bilateral ablation of the STS produced an impairment in the ability to perceive gaze direction (Campbell, Heywood, Cowey, Regard, & Landis, 1990; Heywood & Cowey, 1992). In humans, lesions leading to a specific impairment in the perception of gaze direction are scarce. However, Akiyama et al. (2006a) described the patient MJ, who suffered from a lesion in the right superior temporal gyrus. MJ had difficulty processing gaze direction, while being easily capable of orienting her attention in the direction of an arrow (Akiyama et al., 2006b). Thus, a lesion in her STS caused a deficit in her ability to use biological information about direction (i.e., eye gaze), while her ability to use non-biological directional symbols was spared. According to the authors, this dissociation implies that the STS is specialized in gaze processing, while the FFA and OFA are more involved in face recognition. The case of MJ provides evidence for the dissociation between the processing of invariant and changing facial features, as proposed in Bruce and Young's (1986) model and elaborated by Haxby et al. (2000).

However, there is some evidence that prosopagnosic patients have difficulty processing gaze direction. Campbell et al. (1990) asked two prosopagnosic patients and two healthy controls to discriminate gaze direction. One patient showed a mild deficit in discriminating gaze direction, which was only apparent with small deviations of gaze direction. In contrast, the other patient was unable to discriminate gaze direction. The authors stressed that the discrepancy could not be explained by differences in low-level impairments or differences in the etiology or localization of the lesion. However, subsequent studies with other prosopagnosic patients failed to show impaired perception of gaze direction (Duchaine et al., 2009; Burra et al., 2017). However, it is difficult to reconcile the conflicting results because the latter studies did not provide a detailed examination of the perception of gaze direction.

In the current study, we suggest that abnormal perception of gaze direction in prosopagnosic patients occurs when variations of gaze direction are subtle and difficult to distinguish, but not when variations of gaze direction are obvious and easy to distinguish. In fact, the visible part of the eyes is critical to accurately judge gaze direction. With frontal faces, judgments of gaze direction do not require global processing, but can be based on the comparison of the white surface area (i.e., the sclera) on the left and right side of the eye (Kobayashi & Kohshima, 1997). However, when the head orientation deviates from straight ahead, this strategy is no longer available (Balsdon & Clifford, 2017; Otsuka, Mareschal, Calder, & Clifford, 2014). Some studies with prosopagnosic patients used stimuli with frontal head orientation (Duchaine et al., 2009; Burra et al., 2017), while others used stimuli with deviated head orientation (De Haan & Campbell, 1991; McConachie, 1976; Perrett et al., 1988) and differences between studies may arise from differences in task difficulty caused by head orientation.

To evaluate effects of task difficulty, we systematically assessed the relationship between the processing of face identity (i.e., invariant processing) and the processing of gaze direction (i.e., variant processing) with frontal and deviated head orientation in a well-established case of acquired prosopagnosia, the patient PS. Her pattern of brain damage was particularly informative because two core regions of the invariant network (the right inferior occipital gyrus and the left middle fusiform gyrus) were affected. Critically, the STS was spared bilaterally (Sorger, Goebel, Schiltz, & Rossion, 2007). Consequently, PS suffers from selective impairment in recognizing individuals by their faces (i.e., prosopagnosia) with no other cognitive deficit. Importantly, she shows no impairment of object recognition or low-level visual functions (see Rossion, 2014 for a review). Hence, PS provides the unique opportunity to investigate the perception of gaze direction despite impaired face recognition. While some prior results point to a deficit in the processing of the eye region, the perception of gaze direction was never investigated in detail. Prior studies revealed that PS lost her ability to extract diagnostic information from the eyes to identify familiar faces, which she compensated by using the lower part of the face such as the mouth and external contours (Caldara et al., 2005). Furthermore, in an identity-matching task, PS was not sensitive to differences in the eye area (Burra et al., 2017; Ramon & Rossion, 2010). In addition, PS did not exhibit the reflexive gaze cueing effect (Burra et al., 2017), where attention is rapidly allocated in the same direction as another person's gaze (Driver et al., 1999). Together, these results indicate that the perception of eyes and gaze direction in PS is impaired.

In a previous study, we assessed the perception of gaze direction in patient PS using frontal faces with easily distinguishable gaze directions (i.e., left, right, center). In line with the prior literature, we did not observe any deficit (Burra et al., 2017). However, it is likely that a potential deficit is not noticeable with easily distinguishable stimuli. Rather, a more demanding task is necessary (as in Campbell et al., 1990). Hence, we included gaze directions that were harder to distinguish (up-left, up-right, down-left, down-right), and therefore more demanding (for a similar approach concerning social cognition in patients suffering from degenerative disorders, see Snowden et al., 2003). Furthermore, we included deviated head orientations that require integration of head and gaze cues (Langton, Watt, & Bruce, 2000). In past studies, deficits in gaze perception were more clearly visible with deviated head orientation than with frontal face images (De Haan & Campbell, 1991; McConachie, 1976; Perrett et al., 1988).

In addition to upright faces, we used inverted faces and contrast-reversed faces. The ability to recognize identity is impaired with inverted faces compared to upright faces, mainly because holistic processing is reduced (Jenkins, 1998; Vecera & Johnson, 1995). Perception of gaze direction is also deteriorated with inverted faces (Jenkins & Langton, 2003). However, in comparison with normal subjects, patients with prosopagnosia show less deficit when faces are inverted, suggesting that inverted faces are processed more like objects (Farah, Wilson, Drain, & Tanaka, 1995; Yin, 1970). Notably, the inversion effect is absent in PS (Busigny & Rossion, 2010), consistent with the claim that acquired prosopagnosia is associated with an impairment in holistic processing. To our knowledge, the effect of face inversion on the perception of gaze direction has not been investigated in prosopagnosic patients. We hypothesized that inverted faces would impair perception of gaze direction less in PS than in healthy controls because inverted faces require less holistic perception.

Furthermore, we reversed the contrast of the faces so that the sclera was dark instead of white and the iris was bright instead of dark. Ricciardelli, Baylis and Driver (2000) demonstrated that contrast reversal degraded the perception of gaze direction in healthy participants. The detrimental effect of contrast reversal on perception was larger for gaze direction than head orientation. The authors suggested that these results support the existence of a specialized eye-gazing system that tracks the darkest region of the eye (see Kobayashi & Kohshima, 1997). Interestingly, PS reported using an atypical strategy to infer gaze direction in others where she used exclusively the sclera. Therefore, we predicted that performance would be more strongly impaired in PS than in healthy controls because changing the polarity of the sclera would prevent PS from using her sclera-based strategy. The reason for this effect is that the sclera was dark and could be confounded with the skin of the face.

In sum, we predicted that PS's performance would be impaired on all tasks compared to healthy controls except for the inverted faces condition. For this condition, we predicted no significant difference because the reduction of holistic processing with inverted faces may facilitate performance in PS, whereas it degrades performance in healthy controls.

Method

Participants

The patient PS. PS is right-handed and was 67 years old at the time of testing (born in 1950). She suffered from a closed head injury in 1992 (hit in the back of the head by a bus). PS's clinical history and functional deficit have already been described and investigated in numerous publications (e.g., Burra et al., 2017; Busigny & Rossion, 2010; Caldara et al., 2005; Ramon, Busigny, Gosselin, & Rossion, 2016; Ramon & Rossion, 2010; Rossion, 2014; Rossion et al., 2003; Schiltz et al., 2006; Sorger et al., 2007). The head trauma left her with lesions in regions including the left mid-ventral (mainly fusiform gyrus) and the right inferior occipital cortex, as well as minor damage to the left posterior cerebellum and the right middle temporal gyrus (cf. Figure 1; for details see Sorger et al., 2007).

Following successful neuropsychological rehabilitation (Mayer, Fistarol, & Valenza, 1999; Mayer & Rossion, 2007), her only deficit was impaired face recognition. However, this selective deficit interfered significantly with her daily life. In everyday interactions, she reports using derived semantic representations and various non-facial cues such as the voice, posture, gait, as well as haircut, earrings, external contour of the face and other contextual information to determine a person's identity. In contrast, she never mentioned referring to specific parts of the face such as the eyes, the mouth or the nose to determine the identity of an individual.

Figure 1. Brain damage of the acquired prosopagnosic patient PS. Lesions are localized in the left middle fusiform gyrus (A) and the right inferior occipital cortex (B). R = right hemisphere.

Currently, PS's complaints relate specifically to face processing, both in identity recognition and gaze perception. Regarding perception of the eyes, she describes using the mouth rather than the eyes to recognize others' emotions. She reports exploring faces part by part, unlike a healthy adult who performs a configural analysis in which the different parts of the face are simultaneously integrated into a single representation (Bruce & Humphreys, 1994). Similar to other prosopagnosic patients (Sergent & Poncet, 1990; Tranel et al., 1988), PS did not complain about difficulty in discriminating gaze direction. However, in some real-world situations, she reports having difficulty identifying whether someone is looking at her or not (e.g., when singing in a choir, she does not know whether the conductor is visually addressing her or someone close by). These problems may suggest that gaze perception in PS is abnormal, even though her STS has remained intact. Possibly, the underlying cause is an imperfect integration of the different parts of the face (including the parts composing the eye) to form a holistic/configural percept.

To assess her current cognitive abilities, a neuropsychological examination was conducted. PS had an abnormally low score (24/54) in the *Benton Facial Recognition Test* (BFRT; Benton & van Allen, 1972). This result was confirmed with two more recent tests of face perception. In the *Cambridge Face Memory Test* (CFMT; Duchaine & Nakayama, 2006), her score was severely impaired in the short (32/72) and the long version (37/102). Similarly, her performance was impaired in the *Cambridge Face Perception Test* (CFPT; Duchaine, Germine, & Nakayama, 2007), with a score of 66% in the upright and 88% in the inverted version (chance level at 93.3%). Her performance was also very poor in a test evaluating her capacity to recognize famous people before 1990 (6/20). This test had been created for PS during this study, as her accident happened in 1990. These deficits contrast with her good performance in tasks assessing memory, executive functions, attention, and spatial perception. The aspects of memory that we assessed were verbal working memory (*Hebb span*; Hebb, 1961; *Letter-Number sequencing*; Wechsler, 2008), visuospatial working memory (MEM III; Wechsler, 2001), and anterograde memory (visual recognition in *The Doors and People Test*; Baddeley, Emslie & Nimmo-Smith, 1994, and a reminder of the tasks performed during each interview). The aspects of executive functioning were mental flexibility (*Trail Making Test B*; Tombaugh, 2004), verbal fluency (phonological and categorical fluency), visuospatial fluency (*Five-Points Test*; Lezak, 1995) and inhibition (*Stroop Victoria*; Bayard,

Table 1
Results of PS in the neuropsychological examination

Test	Raw score, performance descriptors
Perceptual processing (screening tests)	
Swiss map recognition	1/1
Placement of regions and cities on the map	6/6
Recognition of a complex drawing (Bœufs de Barbizet)	1/1
Illusory contours identification	3/3, slowed
Semantic associations	4/4
Associations in non-canonical views	4/4
Functional associations	2/2
Categorical associations	2/2
Chimeras discrimination	6/6
Overlapping shapes identification	10/10
Fragmented objects recognition	6/6, slowed
Navon letters	16/16
Ishihara test	2/2
Perceptual processing (standardized tests)	
Benton line orientation (form H)	29/30, normal
Birmingham Object Recognition Battery (BORB)	
Overlapping shapes (test6)	normal (accuracy), slowed (RT)
Face processing	
Benton Facial Recognition Test	24/54, strongly impaired
Cambridge Face Memory Test	32/72 (short version); 37/102 (long) version)
Cambridge Face Perception Test	66% in upright; 88% in inverted conditions
Identification of celebrities known before 1990 (screening)	6/20, impaired
Working memory	
MEM-III (visuospatial)	12, normal, percentile 25
Direct	8, normal, percentile 75
Indirect	4, normal, percentile 15
Hebb span (verbal)	8, normal, percentile > 75
Letter-Number sequencing (WAIS-IV)	20, normal, percentile > 75
Long-term visual memory	
Doors test	21/24, normal, percentile > 75
Part A	12/12, normal, percentile > 75
Part B	9/12, normal, percentile > 75
Executive functioning	
Trail Making Test	
Part A (speed processing)	38'', normal (RT and accuracy)
Part B (mental flexibility)	63'', normal (RT and accuracy)
Verbal fluency (1')	
Phonological (letter M)	8, normal, percentile 10
Categorical (animals)	14, normal, percentile 10
Visuospatial fluency (Five-Points Test)	29, normal, percentile 50
Victoria Stroop test (Interference condition)	22'', normal (RT and accuracy)
Spatial orientation	
Landmark recognition in Geneva (screening)	20/20
Road Map Test	24/32, normal
Cognitive map recall test (CMRT)	
Distances	9/12, normal
Directions	7/12, normal, slowed (RT)

Note. impaired = when PS's performance was inferior to M – 1.96 (SD), was below percentile 5, or was below the borderline score, *normal* = within normal range (within M ± 1.96 SD), *RT = reaction time.*

Erkes, & Moroni, 2009). Attention was assessed by the speed of processing (*Trail Making Test A*; Tombaugh, 2004). The aspects of spatial processing that we assessed were spatial orientation including recognition of familiar landmarks (a screening test created in this study for PS from famous landmarks in her hometown), visuospatial perspective-taking (*Road Map Test*; Money, Alexander, & Walker, 1976), evocations and recall of the cognitive map (*Cognitive Map Recall Test*; Descloux & Maurer, 2018), and low-level visuospatial judgments (*Benton Line Orientation Test*; Benton, Varney, & Hamsher, 1978). Additionally, PS did not show any deficit in recognizing objects, but appeared to be slower than controls in identifying overlapping shapes (*Birmingham Object Recognition Battery*; Riddoch & Humphreys, 1993). Test scores are summarized in Table 1. These tests were administered in the same five sessions where gaze perception was assessed.

Age-matched control participants. Eleven women, matched for age (mean age: 66.4 ± 1.3 years; range: 64 - 68) and education level, participated as healthy controls in the experiments on the perception of gaze direction. All subjects met the main inclusion criteria of the study, as they had no history of psychiatric or neurological diseases and had no cognitive complaints.

Behavioral tests: computerized tests of the perception of gaze direction

PS's gaze direction detection abilities were tested using three analogous tasks in which face stimuli were presented with PowerPoint on a computer monitor.

Upright faces. The stimuli consisted of 48 black-and-white photographs of the faces of two men and two women presented on a black background. The photographs were modified to obtain images of 640 x 480 pixels (size of 16.5 x 16.8 cm in PowerPoint). To produce the required eye deviations, including the upper-left, upper-right, lower-left and lower-right angles, the models were required to look at different markers placed at 30° of deviation from them. Head orientation was frontal in 16 pictures and deviated by 30° in 32 pictures (16 in which the head deviated to the left and 16 in which the head deviated to the right). In all photos, four white squares (3 x 3 cm in PowerPoint) were shown. Each square contained a number (from 1 to 4) written in black. The model looked at one of those squares. Similar to Snowden et al. (2007), these squares were arranged in the corners of the photo (see Figure 2). For all faces, the squares were equidistant from the horizontal axis of the eyes and the vertical axis dividing the nose and mouth. Pictures were presented in the same random order to all participants. In eight additional items, the face was replaced by an arrow pointing in the direction of one of the four squares (see Figure 2). According to Schurz et al. (2015), arrows are classic control stimuli in attention research, and it has been shown that simple arrows can guide attention similar to gaze direction and body posture (Ristic, Friesen, & Kingstone, 2002; Tipples, 2002).

Inverted faces. Subsequently, PS and the healthy controls performed a second task to examine the effect of face inversion on the discrimination of gaze direction. This task included the same images as in the upright face task but with a 180° rotation (see Figure 3).

Reversed contrast. PS and healthy controls then performed a third task to investigate the strategy used by PS to detect gaze direction. Spontaneously, she reported using the sclera to identify gaze orientation. However, with reversed contrast, the sclera becomes dark and the iris becomes light, which would make her strategy ineffective. The same pictures were used as in the upright condition, but with reversed contrast (see Figure 4).

Canonical gaze direction (left, right, up, down). Finally, PS (but not the healthy controls) discriminated gaze direction of pictures showing the same models, but with canonical gaze direction. Thirty-two items were randomly displayed with frontal faces and highly discriminable gaze direction (i.e., left,

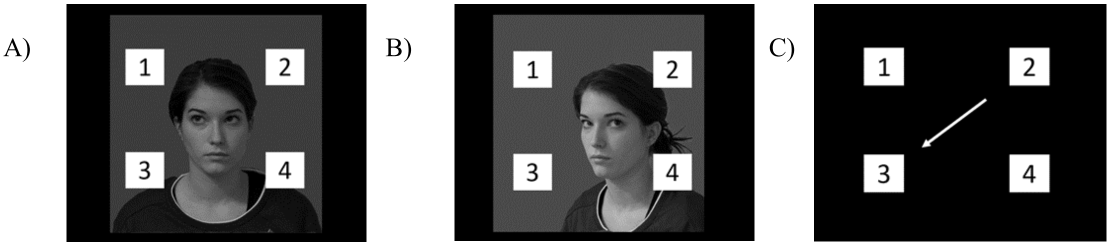

Figure 2. Examples of the upright stimuli. A) frontal face, B) face deviated face by 30° and C) non-biological stimulus. In these examples, the correct answers were 1, 2 and 3, respectively.

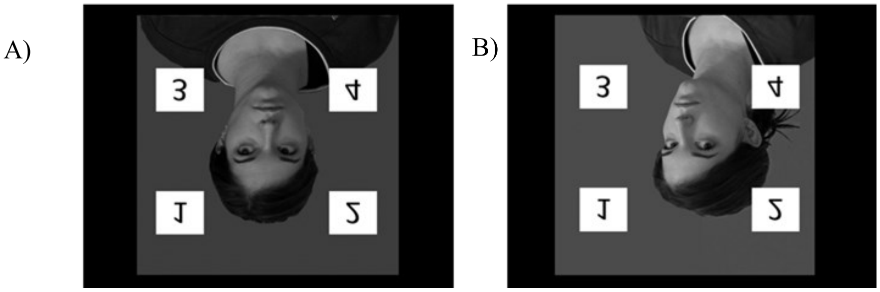

Figure 3. Examples of the inverted stimuli. A) frontal face, B) face deviated by 30º.

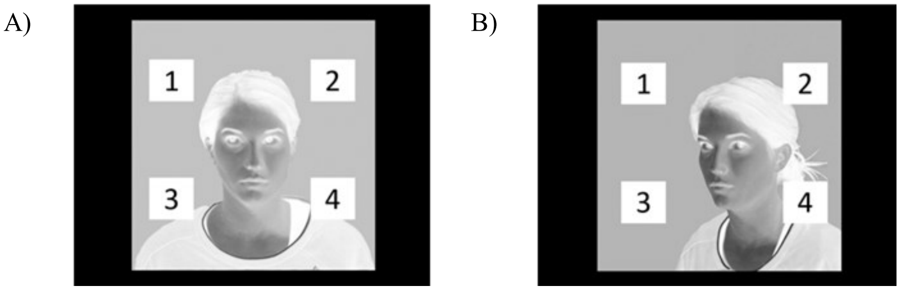

Figure 4. Examples of reversed contrast stimuli. A) frontal face, B) face deviated by 30º.

right, upward and downward gaze direction with 30° of deviation). She was asked to discriminate gaze direction, as in Burra et al. (2017).

Procedure

All participants were informed of the purpose of their participation in the study, as well as their rights, and signed an informed consent form. The procedure was approved by the ethics committee of the University of Geneva and the Geneva Cantonal Ethics Committee. For all experiments, participants were positioned at 54 cm from a 53.1 x 29.9 cm computer screen (1920 x 1080 pixel resolution). Stimulus presentation and response registration were controlled by the experimenter. Stimuli were presented until a response occurred. PS and control participants completed the three conditions in a fixed order. In each condition (upright faces, inverted faces, and reversed contrast), participants were asked to indicate gaze direction as accurately as possible. They were told: "Which of these squares is the person in the center interested in? You can tell me the number or show me with your finger." The experimenter made sure that participants understood that it was necessary to use gaze direction to provide an answer to the question. The experimenter logged the responses on paper.

The order of the stimuli was fixed as follows. The frontal faces were presented first and their order was random but identical for all participants. Then, the deviated faces were presented, and their order was determined in the same way. Conditions were blocked to facilitate performance. The easiest condition (frontal faces) was run first to determine whether PS was able to infer gaze direction when the head orientation was frontal. The eight arrow items were presented at the end of the procedure.

Analyses

PS's performance in the three tasks assessing the ability to detect gaze direction was compared to the matched control group using the modified Crawford and Howell (1998) *t*-test for single-case studies. This method allows for the comparison of a single individual to a group of control persons with a modest *N*. The modified *t*-test evaluates whether the score of the single case differs significantly from that of the control participants by providing a point estimate of the abnormality of the score. In this study, a *p*-value of .05 was the threshold by which the results were considered abnormal. Analyses were conducted with software using the Crawford and Howell (1998) method *SINGLIMS.EXE: significance test and point & interval estimates of effect size and abnormality for a patient's score* (Crawford & Garthwaite, 2002; Crawford, Garthwaite, & Porter, 2010).

A dissociation criterion was also used to examine dissociation between PS's scores on the different tasks. This test reveals the degree of interdependence between different cognitive functions or components (Shallice, 1995). Classically, dissociation is said to occur when a patient's performance on a task X is impaired, while it is preserved on a task Y. In the present study, we examined whether PS's performance on a condition X was impaired relative to the control group, while maintaining intact performance on a condition Y with respect to this same control group. We also evaluated whether PS's performance was impaired compared to the non-clinical sample for both conditions X and Y, and whether there was a significant difference in the degree of impairment on these tasks. The statistical method developed by Crawford and Garthwaite (2005), called *Revised Standardized Difference Test* (RSDT), was used to determine whether dissociation occurred between multiple tasks. This test allowed us to compute the differential deficit between tasks X and Y and to determine whether PS's scores revealed a *strong dissociation*. Strong dissociation refers to situations in which a patient shows significant deficits on tasks X and Y in comparison to the control group, and that in addition, a significant difference is found between tasks X and Y. In other words, strong dissociation is said to occur when performance of the patient is impaired in both tasks but more severely on one than the other (Crawford, Garthwaite, & Gray, 2003). This method reveals whether the difference between the patient's performances on tasks X and Y is unlikely to be caused solely by random factors; this is accomplished by statistically comparing the discrepancy between the patient's scores with the distribution of the differences in the control group. Moreover, this method allows us to determine the proportion of healthy controls who show a difference in performance between the tasks X and Y greater than that found in the single case. In this study, this method was conducted using the software *Dissocs_ES.EXE: classical (frequentist) statistical methods for testing dissociations in single-case studies* (Crawford & Garthwaite, 2005).

Results

Upright faces: frontal vs. deviated head orientation

As displayed in Figure 5, the percentage of correct judgments of gaze direction was lower for PS than for healthy controls. The difference was significant for frontal faces (75% vs. 99%), $t(10) = -11.489$, $p < .001$, and for deviated faces (50% vs. 91%), $t(10) = -9.81$, $p < .001$. The *RSDT* method developed by Crawford et al. (2003) revealed that PS's performance with frontal and deviated faces was significantly different, $t(10) = 2.63$, $p = .03$, and the difference met the criterion for a strong dissociation. In addition, PS made no errors when judging the direction of eight arrows.

Inverted faces: frontal vs. deviated head orientation

As shown in Figure 5, the percentage of correct judgments did not differ between PS and healthy controls for inverted frontal faces (69% vs. 70%), $t(10) = -0.24$, $p = .41$, and inverted deviated faces (38% vs. 51%), $t(10) = -1.38$, $p = .098$. The *RSDT* method revealed that there was no significant difference between frontal and deviated faces for PS, $t(10) = 0.76$, $p = .47$, and thus, there was no dissociation.

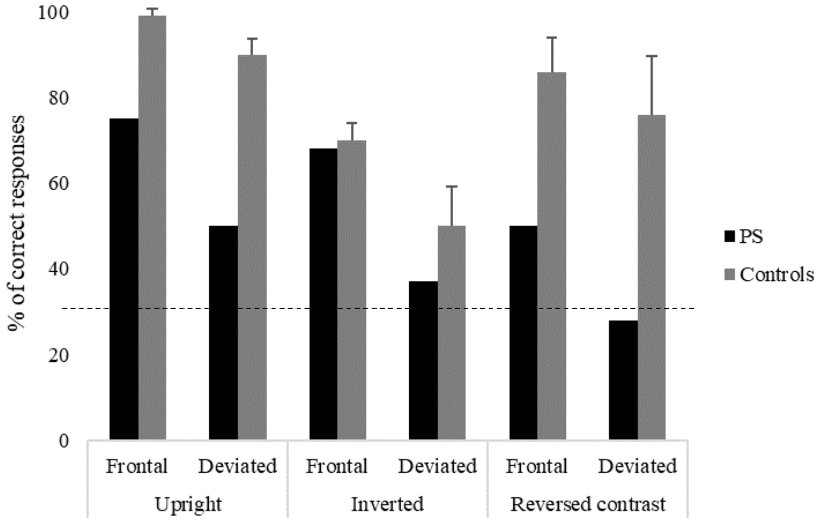

Figure 5. Percentage of correct responses for PS and the control participants as a function of face condition (upright, inverted, reversed contrast) and head orientation (frontal, deviated). The error bars represent the standard deviation of the sample. The dashed line indicates chance level (25%).

Faces with reversed contrast: frontal vs. deviated head orientation

As shown in Figure 5, the percentage of correct judgments was lower for PS than for healthy controls with reversed contrast frontal faces (50% vs. 87%), *t* (10) = -4.428, *p* < .001, and with reversed contrast deviated faces (28% vs 77%), *t*(10) = -3.417, *p* = .003. The *RSDT* method revealed that there was no significant difference between frontal and deviated faces for PS, *t*(10) = 1.011, *p* = .33, and thus, there was no dissociation.

Upright faces vs. inverted faces, collapsed across frontal and deviated

In the following analyses, we collapsed across frontal and deviated head orientation and compared a) upright and inverted faces and b) upright and reversed contrast faces. Means and standard deviations are shown in Figure 6.

For healthy controls, paired sample *t*-test revealed significantly more correct responses for upright (94%) than inverted faces (57%), *t*(10) = 17.03, *p* < .001. For PS, there was also a decrease from upright (58%) to inverted faces (48%), *t*(10) = 6.01, *p* <.001, but this difference was less pronounced than in healthy controls, which fulfills the criterion for dissociation according to the RSDT method.

Upright faces vs. reversed contrast faces, collapsed across frontal and deviated

For healthy controls, a paired sample *t*-test revealed a significantly higher accuracy for reporting gaze direction of upright (94%) than reversed contrast faces (80%), *t*(10) = 3.94, *p* = .003. For PS, accuracy was also higher when judging gaze direction of upright (58%) than reversed-contrast (35%) faces, *t*(10) = 4.73, *p* < .001, but this difference was much larger, which fulfills the criterion for dissociation according to the RSDT method.

Canonical gaze direction (left, right, up, down)

When asked to judge gaze direction in the task using frontal faces with left, right, upward and downward gaze direction, PS was 100% accurate, which replicates our previous results (Burra et al., 2017).

Additional results: error types

For each lateral gaze direction (left, right), there were two vertical gaze directions (upper, lower). To evaluate whether errors were due to choosing the incorrect vertical or lateral direction, we divided errors into same-side errors (with wrong vertical direction) or opposite-side errors (with wrong lateral direction, collapsed across vertical direction).

Upright faces. When the head orientation was frontal, 100% of PS's errors were caused by choosing a response on the same side as the correct answer (same for the control group with a single error). When the head was deviated, 94% of PS's incorrect responses were opposite-side errors. The same pattern of errors was found in the control group, with 94% opposite-side errors.

Inverted faces. When the head orientation was frontal and inverted, 100% of errors made by PS and members of the control group were same-side errors. When the head was deviated and inverted, 80% of

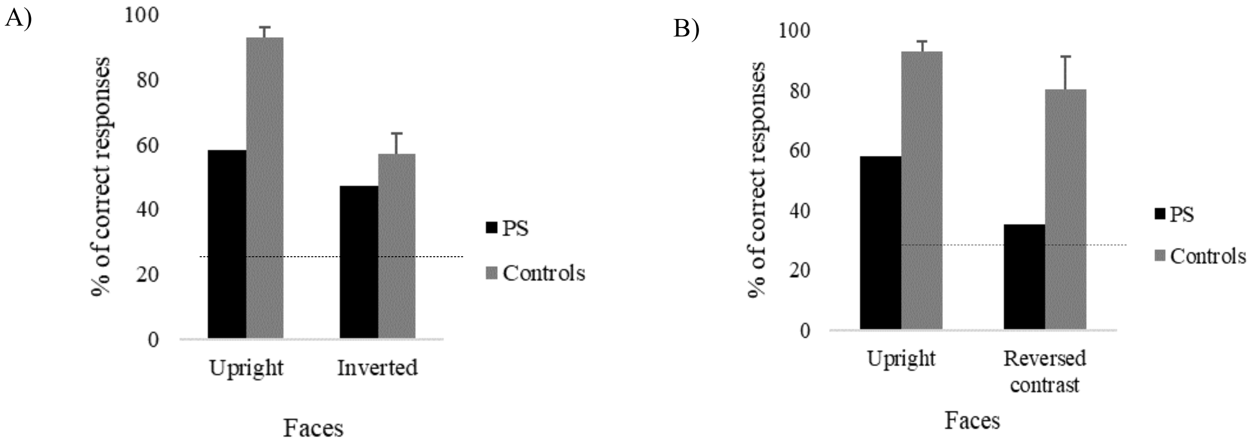

*Figure 6***.** Percentage of correct responses for PS and the control participants. Scores are collapsed across frontal and deviated faces. To complement the text, we repeat results for the upright condition in panels A and B. In the text, we compared A) upright and inverted faces and B) upright and reversed contrast faces. The error bars represent the standard deviation of the sample. The dashed line indicates chance level (25%).

PS's incorrect responses were opposite-side errors. The control group made 53% opposite-side errors.

Reversed contrast. When the head orientation was frontal with reversed contrast, 100% of errors made by PS and members of the control group were same-side errors. When the head was deviated, 86% of PS's and 85% of healthy controls' incorrect responses were opposite-side errors.

In summary, when the head orientation was frontal, for PS and the control group, the majority of errors were same-side errors, showing that participants confused the vertical gaze directions. In contrast, when the head orientation was deviated, the majority of the errors were opposite-side errors, showing that participants confused the lateral direction of gaze.

Discussion

The main goal of this study was to provide a more comprehensive investigation of PS's ability to perceive gaze direction in others. Given her condition of acquired prosopagnosia, PS's difficulty in recognizing face identity has already been described in several studies (e.g., Rossion et al., 2003; Sorger et al., 2007). The present study details an examination of PS's ability to perceive gaze direction with upright, inverted, and reversed contrast faces.

We confirmed that when face stimuli were displayed in frontal view and gaze direction was easy to distinguish (canonical gaze directions: left, right, upward, and downward), PS's performance was at ceiling, which is in line with prior results (Burra et al., 2017; Duchaine et al., 2009). However, when gaze direction was more difficult to distinguish (gaze directed to the upper-left, upper-right, lower-left, and lower-right), the perception of gaze direction with frontal or deviated head orientation was impaired compared to a matched control group. These results imply that task demands are critical to observe a deficit in PS, which is consistent with previous work on other populations (De Haan & Campbell, 1991; McConachie, 1976; Perrett et al., 1988). In other words, the results suggest that abnormal processing of gaze direction only occurs when variations of gaze direction were subtle (upper-left, upper-right, lower-left, lower-right), unlike in previous studies were gaze direction was easy to distinguish (leftward, rightward, upward and downward) (Burra et al., 2017; Duchaine et al., 2009). This pattern of results reflects PS's strategy of comparing the surface area of the sclera on the left and right side of the eye (Kobayashi & Kohshima, 1997). This strategy becomes ineffective when the head is deviated.

While both PS and the control group were less accurate with inverted faces rather than upright faces, the difference was much smaller in PS's results than in the control group's. The decrease in performance with inverted faces is well documented in healthy participants (e.g., Jenkins & Langton, 2003; Rhodes, Brake, & Atkinson, 1993; Yin, 1969). In addition, Rakover and Teucher (1997) found an effect of inversion on the recognition of isolated features of the face, with a greater effect on the eyes than the mouth, suggesting that upright face orientation might be important in the perception of the eyes. However, to our knowledge, no prior research has assessed the effect of face inversion on the ability to detect gaze direction in prosopagnosic patients. In fact, perception of gaze direction requires, at a local level, the ability to decompose the parts of eyes (pupil, iris, sclera). However, at a more global level, it requires that gaze and head orientation to be accurately integrated. In patients with acquired prosopagnosia, the latter process may be impaired. Thus, studies have revealed little impairment in the perception of gaze direction in patients with prosopagnosia when faces were inverted, suggesting that faces are processed more analytically, like objects (Farah et al., 1995; Yin, 1970). For instance, Busigny and Rossion (2010) confirmed that PS's performance was not reduced with inverted compared to upright faces when identity recognition with social and non-social stimuli were evaluated. In contrast, Anaki, Kaufman, Freedman and Moscovitch (2007) found that performance was reduced with inverted compared to upright faces in the prosopagnosic patient DBO when individual faces were discriminated. However, DBO presented an unusual neuropsychological profile compared to other cases of prosopagnosic patients. In the present study, which assessed the identification of gaze direction and not the recognition of faces, the inversion effect was present in control participants and to a lesser extent in PS, who showed just a small decrement with inverted compared to upright faces. The typical deleterious effect of inverted faces on gaze direction identification was therefore not absent in PS, but strongly reduced compared to the control group.

Finally, in order to interfere with PS's strategy of using the sclera to infer gaze direction, she was also presented with reversed-contrast faces where the eyes had a dark sclera and a bright iris. The results showed that PS's perception of gaze direction was significantly reduced compared to the control group and that no dissociation occurred between frontal and deviated head orientation. On the other hand, a strong dissociation between PS's accuracy of judging gaze direction in faces with and without reversed contrast was demonstrated. Both PS and healthy adults were less accurate in perceiving gaze direction when faces were presented with the reversed contrast as opposed to normal contrast, but the effect was amplified in PS. These results support the findings of Ricciardelli et al.

(2000) with a non-clinical population. Ricciardelli et al. showed that reversed contrast had a much more detrimental effect on the perception of gaze direction than on other directional judgments (e.g., judgment of the head orientation), suggesting that a specialized system of eye-gaze tracking exists, where the darkest region of the eye is the directing part. Probably, reversing the contrast of the face impaired PS's performance because the eye region contains contrast boundaries that separate different parts of the eyes and are critical for face detection and recognition processes (e.g., Sormaz, Andrews, & Young, 2013). Reversed contrast makes the sclera easy to confuse with the skin of the face, which may have prevented PS from using her strategy to derive gaze direction from the smaller part of the sclera.

In sum, the results of the present study support the hypothesis that the inability to process faces holistically may account for facial processing deficits in acquired prosopagnosia, as suggested by Busigny and Rossion (2010). This deficit appears to be accompanied by specific difficulties in extracting diagnostic information from the eyes (Caldara et al., 2005). Although the present study shows evidence from only a single case, PS's results challenge several studies in which it was suggested that prosopagnosic patients are able to judge gaze direction (Burra et al., 2017; Duchaine et al., 2009) because the STS is preserved (Hoffman & Haxby, 2000). Conditions in which variations of gaze direction were more subtle revealed deficits that were not apparent with highly distinguishable gaze directions. Finally, PS's results suggest that the approach of Bruce and Young (1986) and Haxby et al. (2000) should be reconsidered. In fact, by increasing the task demands (i.e., by using stimuli with more subtle changes of gaze direction), we revealed a deficit of gaze perception, despite the fact that the STS region of PS's brain was spared. The case of PS therefore confirms that reliable perception of gaze direction also relies on holistic perception, which forms the basis of identity recognition. Our results are therefore consistent with previous research showing that brain regions underlying the processing of identity and facial expressions interact differently depending on task demands (Vuilleumier & Pourtois, 2007).

Further, we would like to mention limitations of the present research. In this study, we systematically assessed the perception of gaze direction in an acquired prosopagnosic patient and a control group. A clear limitation of our study is the generalization of our results to other prosopagnosic patients, knowing the large heterogeneity of this population (Campbell et al., 1990). Future studies should include additional patients or patients suffering from a deficit in face recognition without brain lesions (i.e., developmental prosopagnosia). Moreover, in this study, only female participants have been assessed. Because attention to eye gaze might be different between males and females (Cooney, Brady, & Ryan, 2017), further studies should demonstrate a generalization of this effect in male prosopagnosic patients.

Manipulation of task-demand is often neglected during neuropsychological evaluation. Our study revealed that deficits might remain hidden if the task is too easy. Therefore, we recommend that clinicians manipulate task-demand in order to reveal deficits that may be covered by heuristics (e.g., looking for the smaller part of the sclera).

With respect to rehabilitation, our study shows that the deficit in holistic processing may not only lead to a lack of integration of different parts of the face, but also to a lack of integration of the different parts of the eye. These difficulties would result not only in an inability to recognize familiar faces, but also in an inability to infer social cues such as gaze direction or emotional facial expressions. Therefore, rehabilitation should not only focus on face recognition, but also on various social interactions where patients may miss important cues and suffer from negative psychosocial consequences.

The findings reported here demonstrate that the perception of gaze direction is impaired in a patient suffering from acquired prosopagnosia. However, the deficit was only measurable when the task was difficult. The results are consistent with PS's complaints and suggest that impaired holistic face processing also affects the perception of gaze direction.

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