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Brief Communication

Impairment of holistic face perception following right occipito-temporal damage in prosopagnosia: Converging evidence from gaze-contingency

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ABSTRACT

Gaze-contingency is a method traditionally used to investigate the perceptual span in reading by selectively revealing/masking a portion of the visual field in real time. Introducing this approach in face perception research showed that the performance pattern of a brain-damaged patient with acquired prosopagnosia (PS) in a face matching task was reversed, as compared to normal observers: the patient showed almost no further decrease of performance when only one facial part (eye, mouth, nose, etc.) was available at a time (foveal window condition, forcing part-based analysis), but a very large impairment when the fixated part was selectively masked (mask condition, promoting holistic perception) (Van Belle, De Graef, Verfaillie, Busigny, & Rossion, 2010a; Van Belle, De Graef, Verfaillie, Rossion, & Lefèvre, 2010b). Here we tested the same manipulation in a recently reported case of pure prosopagnosia (GG) with unilateral right hemisphere damage (Busigny, Joubert, Felician, Ceccaldi, & Rossion, 2010). Contrary to normal observers, GG was also significantly more impaired with a mask than with a window, demonstrating impairment with holistic face perception. Together with our previous study, these observations support a generalized account of acquired prosopagnosia as a critical impairment of holistic (individual) face perception, implying that this function is a key element of normal human face recognition. Furthermore, the similar behavioral pattern of the two patients despite different lesion localizations supports a distributed network view of the neural face processing structures, suggesting that the key function of human face processing, namely holistic perception of individual faces, requires the activity of several brain areas of the right hemisphere and their mutual connectivity.

1. Introduction

The scientific literature about the mechanisms responsible for the remarkable ability with which humans can recognize faces has traditionally been characterized by a debate about the relative contribution of an analytical vs. holistic way of processing the visual stimulus. Analytical processing involves selecting first the most diagnostic information from the face in a local part-by-part fashion, bringing the information from different parts together only at a later stage. Evidence for this processing mode in face recognition tasks comes from studies showing that it is indeed possible to recognize faces based on parts only (e.g., Davies, Ellis, and Shepherd, 1977; Sadr, Jarudi and Sinha, 2003) and that facial parts such as the eyes seem to be more important for face recognition than others, as shown by eye tracking studies (e.g., Yarbus, 1967) and response classification experiments (e.g., Gosselin & Schyns, 2001; Haig, 1985). However, other studies show that facial parts are processed interactively, whereby perception of one part is influenced by how we perceive the other parts, as demonstrated by the whole-part face superiority effect (Tanaka & Farah, 1993) and the composite face effect (Young, Hellawell, & Hay, 1987). Along these lines, proponents of the holistic processing view claim that faces are first perceived as a whole rather than a collection of independent parts (Galton, 1883), perhaps as a coarse global representation that can be gradually refined over time (Sergent, 1984; Watt, 1987).

Gaze-contingency is a method that was originally used to investigate the perceptual span in reading (Rayner, 1975) and later in visual scene recognition (van Diepen, Wampers, d'Ydewalle, & Underwood, 1998). Recently, introducing this method in face perception research allowed investigating the amount and type of information that could be simultaneously perceived and potentially used during a face perception task (Van Belle, De Graef, Verfaillie, Busigny, et al., 2010a; Van Belle, De Graef, Verfaillie, Rossion, et al., 2010b). More specifically, Van Belle, De Graef, Verfaillie, Busigny, et al. (2010a) used gaze-contingency to test a well-known

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brain-damaged patient presenting with a face-specific recognition impairment (prosopagnosia, Bodamer, 1947). In a delayed face matching task, the prosopagnosic patient PS (Rossion et al., 2003) was relatively less impaired than typical observers if she was forced to analyze the faces part-by-part through a gaze-contingent window. In contrast, if a gaze-contingent mask obstructed only her fixated part, the patient's performance decreased dramatically as compared to normal observers.

These results led to the conclusion that the cause of PS' face recognition impairment is the inability to perceive individual faces holistically, supporting the view that holistic perception is necessary for visual expertise in processing faces.

So far, these findings were obtained in only one case of prosopagnosia, a patient who has distributed lesions, including a large lesion in the right inferior occipital cortex, in the left middle fusiform gyrus, and to a smaller extent in the right middle temporal gyrus (Sorger, Goebel, Schiltz, & Rossion, 2007). Nevertheless, there is evidence that holistic perception of individual faces is primarily a function of the right hemisphere (e.g., Hillger & Koenig, 1991; Schiltz & Rossion, 2006), and it has been suggested that an impairment of this function is a common characteristic of all cases of prosopagnosia following brain damage (Ramon, Busigny & Rossion, 2010; see also Barton, Press, Keenan, & Connor, 2002). To provide further evidence for these views, and more generally help getting a clearer view on the neural mechanisms responsible for holistic processing, the present study reports the test of the same gaze-contingency experiment on another case of acquired prosopagnosia (GG, Busigny et al., 2010). Contrary to PS, GG has a single lesion, unilaterally in the right hemisphere, which encompasses a large section of the medial section of the ventral occipito-temporal cortex including the lingual, medial fusiform, and parahippocampal gyri. Despite the extent of the brain damage, his object recognition is entirely preserved, so that, like PS, GG suffers from a face-specific visual agnosia ("pure prosopagnosia", see Busigny et al., 2010).

2. Materials and methods

GG is a right-handed male born in 1942 who suffered from brain damage after a cerebral vascular accident in 2002. His remaining complaints are a left hemianopia and prosopagnosia. GG's object recognition and perception is intact, even for tasks requiring holistic processing of objects (for more details about GG's case, see Busigny et al., 2010).

The course of a trial in the delayed face matching task was identical to the study with PS (see Fig. 2 in Van Belle et al., 2010a). Each trial started with a fixation cross on the left of the screen. Upon fixation of this initial fixation cross, a reference face appeared for 4 s, followed by two faces side by side, from which one of the two matched the reference face. In one third of the trials, the fixated face was completely visible (full view condition). In one third of the trials the fixated face was visible through a small gaze-contingent window, allowing only to see one part of the face at a time (e.g., one eye, or the nose, or the mouth, etc.). In the last third of the trials the fixated area was covered by a gaze-contingent mask, so that the observer could not rely on the fixated feature, therefore reducing the reliance on part-based (analytical) processing. An average grayscale face always covered the non-fixated face.

As in the gaze-contingency study of PS (Van Belle et al., 2010a), the stimulus set contained 10 male and 10 female faces (KDEF database, Lundqvist, Flykt, & Öhman, 1998) from which the external features were cropped but with preservation of the head shape. The faces were randomly combined in pairs of two males or two females.

Stimuli were displayed using Presentation software, on a 22″ Sony Trinitron monitor at a viewing distance of 58 cm with a spatial resolution of 1600 by 1200 pixels and a refresh rate of 85 Hz. The height of the faces was 11°, the distance between the inner borders of the faces was approximately 6° and the elliptical window and mask subtended 7° horizontally by 5.5° vertically. Both stimulus display and response registration were handled by an Intel Centrino vPro. Eye movements were registered with an SR Research Eyelink 1000 remote eye tracker at a sampling rate of 250 Hz and with gaze position error smaller than 0.5°. Head movement was restricted by a chin and head rest. GG's performance was contrasted with the performance of 7 age- and gender-matched control participants with normal or corrected to normal visual acuity and with normal performance (range: 39/54 to 48/54, average 42.5) on the computerized version of the Benton Face Recognition test (Benton & Van Allen, 1968). Each participant completed 4 blocks of 45 trials (15 trials per viewing condition, in random order).

The effect of the viewing condition (full view, central mask, or window) on accuracy and response times was investigated with an analysis of variance (ANOVA), including only trials resulting in correct responses for the response times. The contrasts between the individual viewing conditions were assessed with a Tukey multiple comparisons analysis. The direct comparison between GG and control participants was assessed using Crawford and Howell's method for the analysis of single case neuropsychological data (Crawford & Howell, 1998).

3. Results

3.1. Behavioral data

For normal observers, performance differed significantly between conditions (main effects: accuracy rates: $F(2, 12) = 8.45$; $p = .005$, RT: $F(2, 12) = 11.53$; $p = .0016$, number of fixations: $F(2, 12) = 16.97$; $p = .0003$). Specifically, performance was higher in full view than with the mask (Accuracy: $t(12) = 3.88$; $p = .006$, RT: $t(12) = 4.78$; $p = .0012$, fixations: $t(12) = 5.78$; $p = .0002$), and the window ($t(12) = 3.13$; $p = .022$, $t(12) = 2.77$; $p = .042$, $t(12) = 2.28$; $p = .098$, respectively). Accuracy and response times in the mask and window conditions did not differ from each other (Accuracy: $t(12) = 0.75$; $p = .74$, RT: $t(12) = 2.01$; $p = .15$), although participants made more fixations with the mask than window ($t(12) = 3.51$; $p = .011$) (Fig. 1).

In contrast, GG's accuracy was significantly higher with full view, (parametric bootstrap test with 10,000 repetitions; $M = .78\%$; 95% CI = [.667; .883]) and with a window ($M = .77\%$; CI = [.650; .867]) than with a mask ($M = .62\%$; CI = [.500; .733]). The difference between the full view and window conditions was not significant.

GG's response times and number of fixations (main effect: RT: $F(2, 177) = 32.89$; $p < .0001$, fixations: $F(2, 177) = 44.15$; $p < .0001$) followed the same pattern. He was significantly slower and made more fixations with the central mask than with full view (RT: $t(177) = 7.74$; $p < .0001$, fixations: $t(177) = 8.61$; $p < .0001$), or with the window (RT: $t(177) = 5.96$; $p < .0001$, fixations: $t(177) = 7.57$; $p < .0001$). Response times and number of fixations with the window did not significantly differ from those in full view (RT: $t(177) = 1.79$; $p = .19$, fixations: $t(177) = 1.04$; $p = .55$).

GG's accuracy was lower than the control participants only with full view (full view, $t(7) = 2.027$; $p = .045$; mask, $t(7) = 1.14$; $p = .15$; window, $t(7) = 0.72$; $p = .25$). However, his response times and number of fixations were higher with the mask condition (RT: $t(7) = 2.75$; $p = .017$, fixations: $t(7) = 4.40$; $p = .002$), but not with full view (RT: $t(7) = 0.15$; $p = .44$, fixations: $t(7) = 64$; $p = .27$), nor with the window (RT: $t(7) = 0.29$; $p = .39$, fixations: $t(7) = 0.31$; $p = .38$).

In order to combine accuracy and response times in one variable and to assess the magnitude of the decrease of performance between the full view and the two experimental conditions, we calculated two indices of experimental effect for GG and each control participant. First, we computed the efficiency (accuracy divided by average response times of the correct trials) for the three conditions. Next, we calculated the relative decrease in performance, between the full view and the mask ((full − mask)/average (full, mask)) and between the full view and the window ((full − window)/average (full, window)).

Fig. 2 shows the result for each participant separately: GG is more affected than the controls by the mask ($t(7) = 2.26$; $p = .033$) as evident from a stronger decrease in performance than the controls. In contrast, GG's decrease in performance caused by the window condition falls perfectly in the range of the controls' ($t(7) = 0.34$; $p = .37$).

3.2. Eye movements

Fig. 3 shows heat maps of the amount of fixations on each position in the stimulus. On average, control participants' gaze is located primarily in the eye region, more specifically, in the area in between the two eyes. GG's preferred fixation location, on the contrary, is the

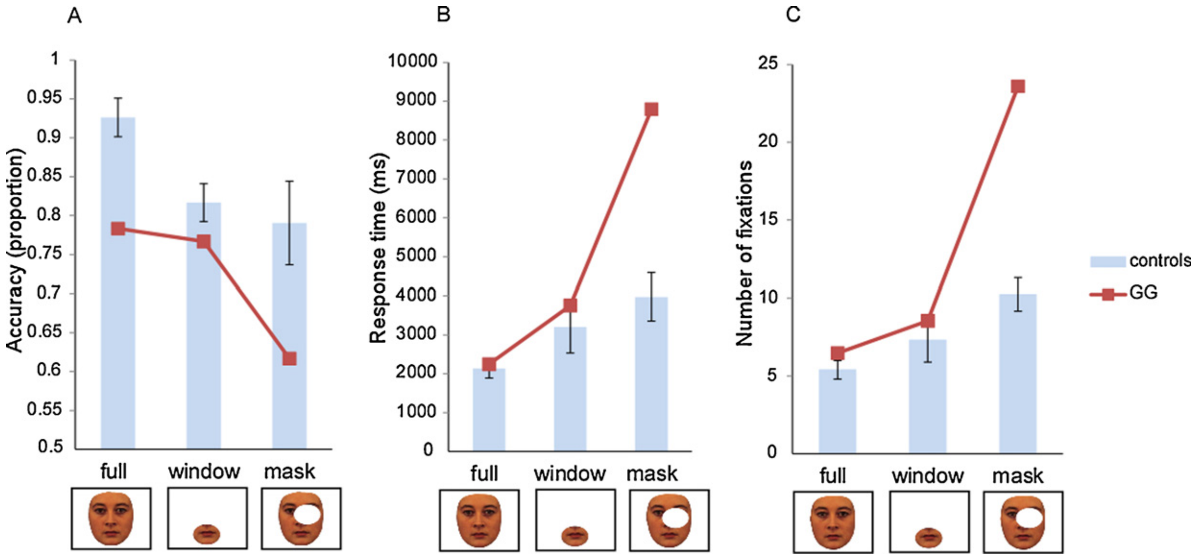

Fig. 1. Accuracy (A), response time (B) and number of fixations prior to response (C) of GG and the control participants for each viewing condition.

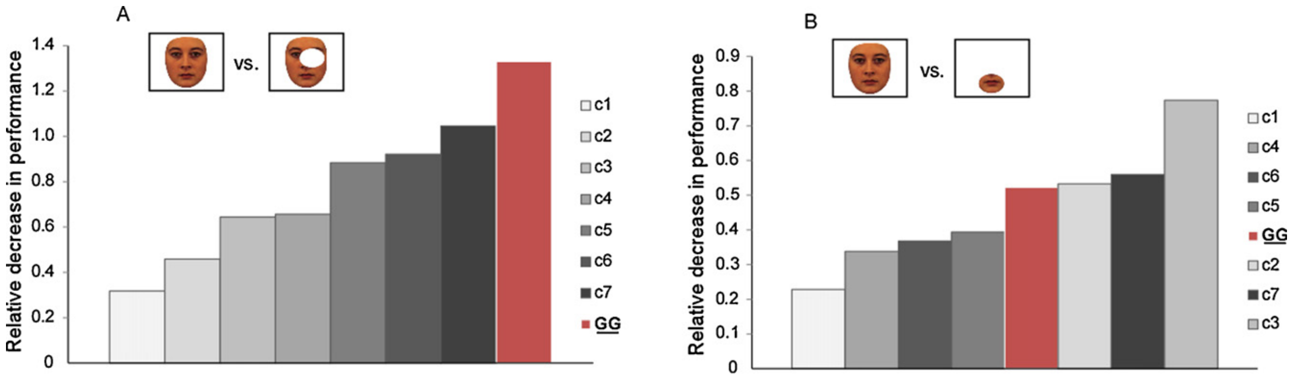

Fig. 2. Decrease in performance (efficiency) due to (A) mask or (B) window, relative to the average performance level for each participant separately.

mouth, and, to a lesser extent also the eye region, although in that case, he seems to fixate each eye in itself rather than in between the two eyes.

The correlation, and thus the similarity, between the fixation pattern in full view and that in the two other viewing conditions was calculated for each participant separately. Only the image regions containing a face stimulus were taken into account for the correlations. The correlation between the fixation patterns in full view and mask appeared to be significantly larger for controls ($r = .822$) than for GG ($r = .665$, $t(6) = 2.19$; $p = .035$). However, the fixation patterns in full view and with a window were not significantly different both for the controls ($r = .856$) and for GG ($r = .774$, $t(6) = 1.02$; $p = .173$).

4. Discussion

Like the previously reported case of acquired prosopagnosia PS, GG has a strong impairment with the central mask condition when matching/discriminating individual faces. This condition prevents using the fixated part, and thus promotes reliance on

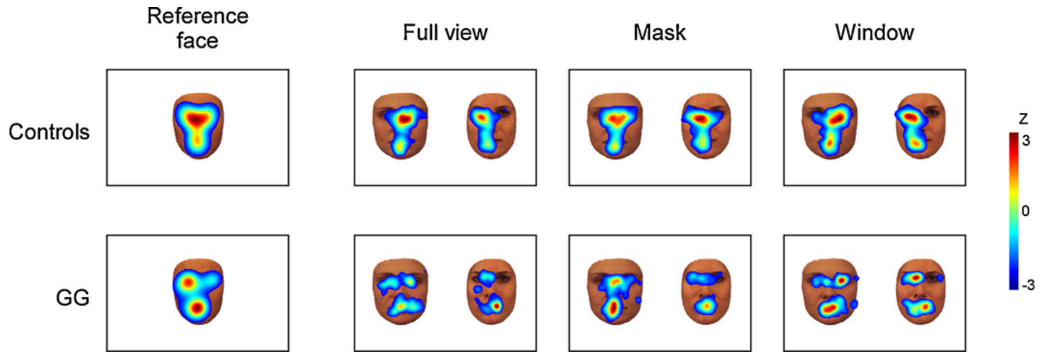

Fig. 3. Heat maps of the fixation pattern of GG and the control participants during the task, on the reference face that is presented first for 4 s, and on the two faces that are presented side-by-side after a delay. Heat maps are computed by adding a Gaussian patch for each fixation, standard normalizing this sum, and colour coding the resulting *Z*-scores as indicated in the scale.

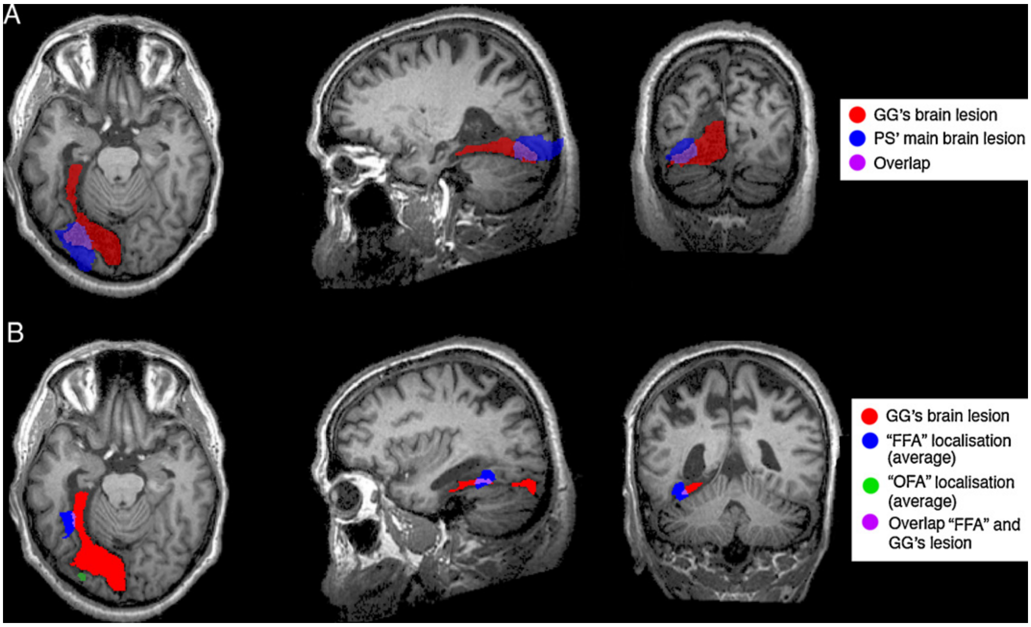

Fig. 4. (A) Extent of GG's brain tissue damage, which concerns the medial section of the right ventral occipito-temporal cortex on a Talairach-normalized T1 image (see also Busigny et al., 2010). The main right hemisphere lesion of the previously described case of prosopagnosia PS (Rossion et al., 2003; Sorger et al., 2007) is defined on her Talairach-normalized brain and represented in blue. The overlap between the two lesions represents 9.8% of GG's lesion. Note that the size of the lesion could even be larger because it was estimated using a conservative approach, its exact size being difficult to assess due to the merging of the lesion with the ventricles. (B) GG's brain lesion is represented with respect to the localization of two well-known face-sensitive clusters (right "FFA" and right "OFA") as defined in a group analysis from a large set ($N = 40$) of right-handed participants by the contrast {(faces-objects) and (faces-scrambled faces)} (Rossion, Hanseeuw, & Dricot, in press). Note that GG's lesion does not include the right OFA and concerns only a fraction of the averaged right FFA. According to a rough estimation (superimposition of the damaged area onto the segmented brain of 19 brains of normal observers as tested in Gentile and Jansma, 2010), the patient's lesion would concerns about half (45%) of white matter. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

holistic perception to realize the task. In contrast, GG showed a similar performance level as controls in the window condition, the condition that forces relying on a single part at a time. This observation demonstrates again the key role of holistic perception for normal face recognition, in showing that forced reliance on part-based processing results in a performance level of normal observers comparable to that of a case of prosopagnosia.

Note that this performance pattern is unlikely to be explained by GG's left hemianopia (see Fig. 1A in Busigny et al., 2010), since his response pattern is similar to PS, who has no visual defect in the periphery but a paracentral scotoma falling within the window area (see Van Belle et al., 2010a). Also note that, contrary to the study with PS, normal observers here did not perform better with a mask than with a window, and, if anything, the non-significant trend was in the opposite direction (Fig. 1). This is probably due to the larger size of window and mask (increase of approximately 15%), relative to the size of the face, in the current study compared to the previous study with PS. Alternatively, it could also be due to the difference in sex (males here vs. females in the previous study) and age of the controls (older in the present study). Also, note that the performance of more than 80% correct responses in the window condition confirms previous findings that recognition based on analyzing one part at a time is indeed possible. However, this performance level is also attained by the prosopagnosic patient.

Importantly, our observations do not imply that parts are not important for normal face perception, only that analyzing the face stimulus in a part-based (analytical) fashion is generally (although not always, see Rivest, Moscovitch, & Black, 2009) well preserved in acquired prosopagnosia, and thus does not appear to be at the heart of what makes normal observers experts at face recognition. The ability to perceive all parts in a simultaneous fashion, however, seems to be the key difference between face perception of a prosopagnosic patient, and a normal observer.

Furthermore, by clearly demonstrating with gaze-contingency that GG does not perceive an individual face holistically, the data reinforce the behavioral findings reported in Busigny et al. (2010), showing that GG does not process facial parts interactively, as evident from the absence of significant composite face, part-whole and face inversion effects for this case of prosopagnosia.

GG's fixation pattern is also in agreement with this account of the results in terms of a lack of holistic processing, since there is an increased amount of fixations on the mouth and on the eyes themselves, compared to a more central gaze preference of control participants. The preference for gaze fixations on the mouth was also found with PS (Orban de Xivry, Ramon, Lefèvre, & Rossion, 2008), in line with previous observations in PS and another case of acquired prosopagnosia (LR) that the mouth has become the most diagnostic individual part for individualizing faces in such cases (Bukach, Bub, Gauthier, & Tarr, 2006; Caldara, Schyns, Mayer, Smith, Gosselin, & Rossion, 2005). In contrast, the reason why normal observers fixate in between the eyes could be because it would be the centre of mass of the face, and therefore the most efficient gaze position to simultaneously perceive all parts of the face (Hsiao & Cottrell, 2008; Orban de Xivry et al., 2008).

Finally, the present study further underlines the very similar nature of functional impairment for the two different cases of acquired prosopagnosia PS and GG. This supports the view that holistic (individual) face perception impairment may be a general – and fundamental – characteristic of acquired prosopagnosia (Ramon et al., 2010). Moreover, since the two patients do not present the same pattern of brain damage (see Sorger et al., 2007 for PS, and Busigny et al., 2010 for GG; see also Fig. 4 for a comparison of the two patients' lesions), the present observations have implications for our understanding of the neural basis of face recognition. PS' lesions concern mainly the right lateral occipital cortex, comprehending the right 'Occipital Fusiform Face Area' (OFA) as found in the normal brain, but she also has a lesion in the middle fusiform gyrus of the left hemisphere, comprehending the left 'Fusiform Face Area' ('FFA', Sorger et al., 2007). However, her right middle fusiform gyrus is intact and shows face-sensitive activation (right FFA, Rossion et al., 2003). In contrast, GG's lesion is restricted to the ventro-medial section of the right hemisphere, sparing largely the lateral occipital cortex. It encompasses most of the parahippocampal and precuneus gyri, and only a restricted medial portion of the fusiform gyrus (Busigny et al., 2010). There is only a small overlap between the lesions of the two patients for their Talairach-normalized brains in the right inferior occipital gyrus, with PS' damaged tissue concerning only 9.8% of GG's unique lesion (Fig. 4A).

These observations lead to two conclusions. First, the right unilaterality of GG's brain damage further supports the view that a left hemisphere damage, as in PS, is not necessary, for holistic perception of individual faces, while the right hemisphere might well be critical not only for face recognition difficulties in general (Sergent & Signoret, 1992; Tranel, Vianna, Manzel, Damasio, & Grabowski, 2009) but for this function in particular. Second, although the absence of functional imaging data in patient GG demands caution in drawing conclusions about the functional state of the regions, there is no overlap between his lesion and face-sensitive responses in the normal brain in the right inferior occipital gyrus, where the right OFA is usually disclosed (Fig. 4B). This observation stands in contrast to PS' brain damage, which encompasses the cortical territory of the right OFA (Fig. 4A, and Rossion et al., 2003). Interestingly, also in contrast with PS, GG's lesion overlaps partly with an average localization of the right FFA (Fig. 4B), suggesting that this area might be partly damaged (see also Fig. 25 in Busigny et al., 2010). Moreover, GG's right ventro-medial lesion appears to overlap largely with white brain matter of the normal brain (Fig. 4B). It is thus also likely to concern putative anatomico-functional connections between the two areas. Connections between these areas and the anterior inferior temporal cortex, either through the inferior longitudinal fasciculus (ILF, Catani, Jones, Donato, & Ffytche, 2003), a fiber pathway coursing along the inferior surface of the brain from the occipital pole to until the temporal pole, and long proposed as a possible substrate for prosopagnosia (Fox, Iaria, & Barton, 2008; Meadows, 1974; see also Thomas, Avidan, Humphreys, Jung, Gao, & B, 2009), or to U-shaped projections connecting adjacent gyri along the inferior surface of the temporal lobes, are also likely to be partially damaged.

Taken together, the observations of a similar behavior for these two cases of pure prosopagnosia with different lesions localization suggest that even if different areas of the right hemisphere cortical face network may play different roles in the normal brain, these areas are functionally interdependent. For instance, damage to the right inferior occipital gyrus may lead to abnormal face processing in the right middle fusiform gyrus (no release to adaptation to individual faces in the FFA, Schiltz & Rossion, 2006), or vice versa (diaschisis). According to this view, the function that would be impaired first and foremost following damage to the network would be a function that relies on the integrity of the whole network of visual areas sensitive to faces. This function might be the holistic perception of individual faces, the highest level of face processing expertise, as illustrated here and previously with the original approach of face gaze-contingency.

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