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Original Article

Acquired Prosopagnosia with Structurally Intact and Functional Fusiform Face Area and with Face Identity-Specific Configuration Processing Deficits

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Abstract

Prosopagnosia or loss of face perception and recognition is still poorly understood and rare single cases of acquired prosopagnosia can provide a unique window on the behavioural and brain basis of normal face perception. The present study of a new case of acquired prosopagnosia with bilateral occipito-temporal lesions but a structurally intact FFA and OFA investigated whether the lesion overlapped with the face network and whether the structurally intact FFA showed a face selective response. We also investigated the behavioral correlates of the neural findings and assessed configural processing in the context of facial and non-facial identity recognition, expression recognition and memory, also focusing on the face-selectivity of each specific deficit. The findings reveal a face-selective response in the FFA, despite lesions in the face perception network. At the behavioural level, the results showed impaired configural processing for facial identity, but not for other stimulus categories and not for facial expression recognition. These findings challenge a critical role of the FFA for face identity processing and support a domain-specific account of configural processing.

Keywords: body, configural processing, emotion, FFA, prosopagnosia

Introduction

Recognition of identity and emotion conveyed by the face is normally an effortless process, except for individuals suffering from a deficit in face recognition or prosopagnosia, (Bodamer 1947). Prosopagnosia in adulthood or acquired prosopagnosia (AP) typically follows from acute brain damage, for example, stroke. AP has considerable theoretical relevance for understanding which brain areas and networks are critically involved in normal face perception. In functional models of intact face and facial expression perception, the fusiform face area (FFA) occupies a central role (Kanwisher et al. 1997; Haxby et al. 2000; Corrow et al. 2016). The role of FFA is typically defined by its face selectivity. The FFA distinguishes faces from other object categories and process them accordingly. Just what this implies is still unclear.

The core function of the FFA is presumably perception of person identity (Haxby and Gobbini 2011; Tsantani et al. 2021) and lesions in the anatomical area corresponding to the FFA are presumed to affect severely face identity recognition behavior. Yet, early reports of patients with AP showed that prosopagnosia is not always linked with FFA lesions (Hadjikhani and de Gelder 2002). A recent meta-analysis of 44 AP cases revealed that in 29 (66%) of them the lesion intersected the region of the FFA and thus that in 15/44 AP cases (34%), the FFA location appeared structurally unaffected. However, all 44 lesion locations were functionally connected to the FFA in healthy subjects (Cohen et al. 2019). Interestingly, this study thus showed that in about one third of AP cases, the lesion did not encompass the FFA itself but instead included the areas connected to the FFA. Such a pattern is in line with the notion that the behavioral correlates of a lesion do not reflect a deficit of the functional role attributed to the lesioned area but are related on the integrity of the functional network that area is part of (Huang et al. 2020). These findings raise the question whether damage to the face network, but not to the FFA itself, is at the origin of the face perception deficit. To address this issue, the function of this area and the visual processes defining it must be explored in more detail, comparing faces and objects (de Gelder and Rouw 2000a). In the present study, we address this issue and investigate both the structural and functional integrity of the FFA region in a new case of AP focusing

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on the underlying perceptual mechanisms at stake in face perception.

At the behavioral level, the face-selective response of the FFA has been linked to a specific processing mechanism referred to as configural processing. Configural processing is understood to be the processing of the spatial relations among the features of a stimulus, that is, for a face: two eyes above a nose above a mouth and there is evidence that this function is supported by the FFA (Maurer et al. 2002). Patients with prosopagnosia have occupied a central place in elucidating the cognitive functions of the FFA, including its configural processing, but that role is still largely underspecified (Burton et al. 2015). It is an open question whether configural face perception generates a representation that allows access to face memory and to face attribute recognition like emotion, gender, age.

We combined structural and functional neuroimaging with behavioral methods to investigate the face specificity and the processing mechanism specificity in EP. We focused on core questions in the literature. First, we address the hypothesis that AP with structurally intact FFA results from a dysfunctional FFA. Second, we test the hypothesis that the functionality of the FFA is behaviorally reflected in failure of configural processing. Configural processing is classically investigated by means of two tasks, one measuring the inversion effect, that is, contrasting the performance for upright versus inverted faces (Yin 1969) and the part-whole effect, that is, a stimulus part is recognized less well in a meaningful than in a scrambled stimulus (Tanaka and Simonyi 2016). The former refers to the fact that canonically oriented faces are better recognized than upside down presented ones and the latter denotes a pattern of superior recognition of the whole compared to its parts (or more precisely, that recognition of a part is superseded by recognition of the whole). Configural processing as measured by face inversion is associated with FFA activity (Yovel and Kanwisher 2005; Watson et al. 2016). While a deficit in configural processing is most often viewed as the behavioral hallmark of impaired face perception and recognition, the relation between the behavioral deficit in configural processes and damage to the FFA and/or damage only to connected areas and the face network is still poorly understood (Righart and de Gelder 2007; Burton et al. 2015).

A central concern in measuring configuration processing, its face specificity in relation to the function of the FFA is category selectivity. While configural processing has been investigated predominantly for faces, it is also important for object recognition as was already described in the original study of the inversion effect (Yin 1969). Thus, the issue of the face specificity is not just about category selectivity but also concerns the processes involved in face identity. This means that the inversion and the configuration effect need to be assessed also in control object categories. In this context an interesting control category is bodies (Righart and de Gelder 2007; Van den Stock et al. 2008; Moro et al. 2012). Faces share more attributes with bodies than with most other stimulus categories as faces and bodies both convey information about identity, age, sex and emotion. Faces and bodies are both processed configurally, as shown by the inversion effect originally reported for face perception but later also for body perception (the "body inversion effect" (Reed et al. 2003; Meeren et al. 2008; Brandman and Yovel 2010; Yovel et al. 2010; Robbins and Coltheart 2012). It is at present unclear how configuration computations that are most typical for faces but equally involved in normal object recognition, are damaged by lesions to either the FFA or to the face network. At the neural level, the fusiform body area (FBA) is very closely related to the FFA (Hadjikhani and de Gelder 2003; Peelen and Downing 2005). This makes bodies an important control category for establishing face specificity of the prosopagnosic deficit.

Furthermore, it is still an open question if impairments of face identity recognition, whether or not due to lesions to FFA and/or the face network, spill over into difficulties in recognition of facial expressions (Calder and Young 2005; Peelen et al. 2009; Van den Stock 2018). This question has not been on the forefront of prosopagnosia studies as they have been dominated by models of face perception where emotion is not part of the core face perception network (Bruce and Young 1986; Haxby et al. 2000). Yet there is evidence of interdependence between emotion and identity processing, rather than serial or parallel separate processing routes (Kaufmann and Schweinberger 2004; Van den Stock and de Gelder 2014; Van den Stock 2018). The finding that perception of facial expressions is orientation specific indicates that configuration perception plays a role in expression perception as it does in identity perception (de Gelder et al. 1997; Calvo et al. 2012). It has been reported that emotional cues influence face identity processes, such as in case PS who not only benefited from emotional facial expressions in an identity visual search task, but emotional cues influenced her scores more than seen in controls. Similarly, when asked to detect changes in faces or houses, she was better able to detect changes in fearful rather than neutral faces (Peelen et al. 2009). In line with this, another AP case showed only covert facial emotion processing as overt facial expression recognition was impaired, but vocal expression recognition was influenced by facial expressions (de Gelder et al. 2000). In addition, five APs with occipito-temporal lesions were better at matching faces based on emotion than on identity and viewing emotional expressions triggered activation in face responsive areas including the fusiform gyrus, superior temporal sulcus, orbitofrontal gyrus and amygdala (de Gelder et al. 2003). Similarly, it is an open question whether configural face perception generates a representation that allows access to face memory. Furthermore, we address the identity and emotion is issue by assessing memory for identity of neutral and emotional faces.

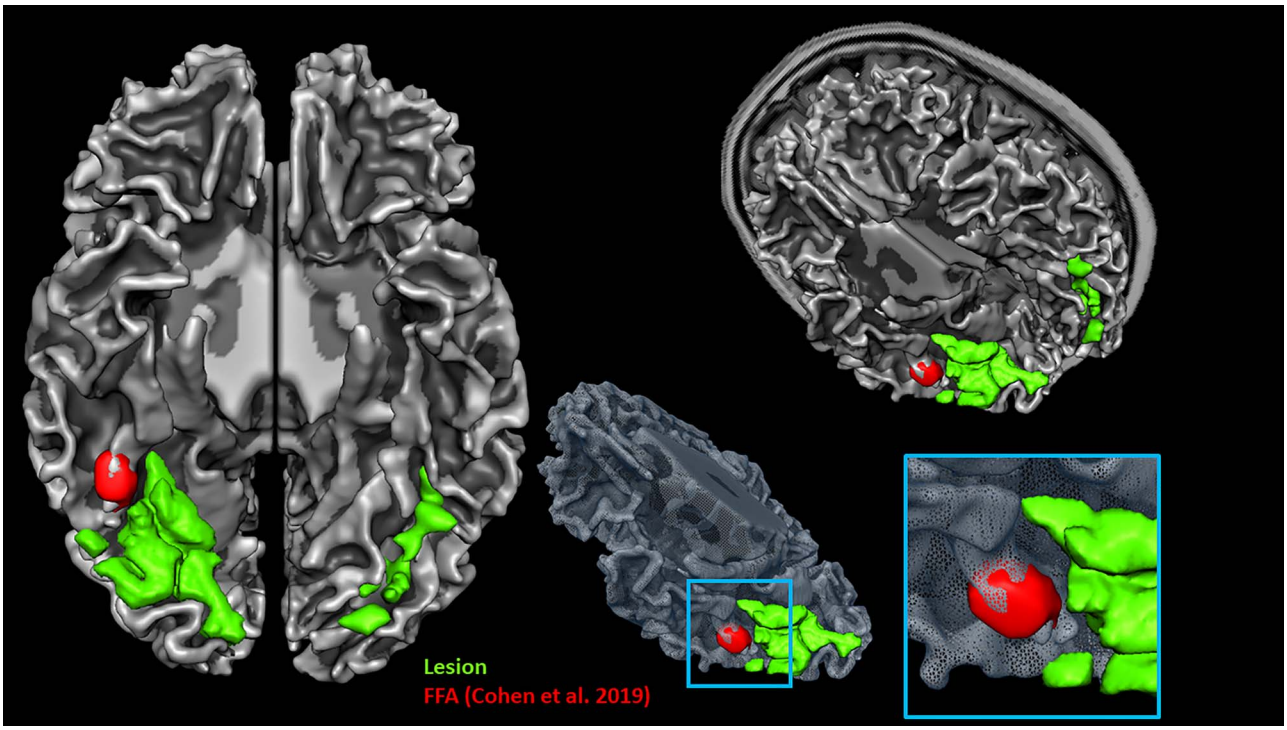

Figure 1. EP's lesion topography. Canonical and wireframe renderings of EP's cortical (gray) and lesion (green) reconstruction, topographically related to the FFA (red) defined by Cohen et al. (2019).

To summarize, our study aimed to answer the following specific research questions. First, we asked whether the structurally intact FFA of EP shows face-selective activation. Secondly, we assessed whether the configuration processing is intact and if impaired, whether the impairment is specific for faces. Finally, we investigated whether face identity specific configural processing impacts facial expression perception and memory.

Materials, Methods and Results

The study was carried out in accordance with the Declaration of Helsinki and informed consent was obtained. The Ethical Review Committee Psychology and Neuroscience of Maastricht University approved the study.

Patient EP

EP (male, right-handed, aged 46 at the time of testing) suffered two successive cerebrovascular incidents within a one day interval in October 2012 damaging areas in right and left occipitotemporal cortices, but sparing the FFA. The lesion in the right hemisphere covers the lingual, fusiform and a small part of the inferior temporal gyrus, with the center of the lesion localized in the mid fusiform gyrus. The lesion extends dorsally into the white matter, affecting the ventral section of the optic radiation. In the left hemisphere, the lesion is more confined and comprises only the middle and posterior section of the fusiform gyrus (see Fig. 1 and Bobes et al. 2021). The major cognitive sequelae consisted of prosopagnosia, including difficulty recognizing the face of his spouse and of close relatives.

Visual Field Mapping

EP's visual field was tested using a computerized visual field mapping task. A high-resolution visual perimetry was administered the same day as fMRI testing with stimuli consisting of small white circles (1°; stimulus luminance 95 cd/m^2) presented against a dark background (2 cd/m^2) on a 24-inch computer monitor. Stimuli were presented one at a time for 300 ms at each of 64 different positions (16 stimuli for each visual quadrant) with onset and offset signaled by two different sounds and at a 3 s inter-stimulus interval. EP was instructed to fixate and verbally report the detection of any stimulus and its location on the screen. This procedure enabled us to map the patient's visual field within an ideal grid spanning 25° of horizontal and 20° of vertical eccentricity. A similar visual perimetry was performed with flickering (20 Hz), instead of static, stimuli. EP showed a scotoma in the upper left visual quadrant spanning approximately 15° horizontally from the center and 10° vertically.

Clinical Tests of Face and Object Recognition

Low level vision was assessed by means of subtests of the Birmingham Object Recognition Battery (BORB) (Riddoch and Humphreys 1993). EP scored within the normal range on most tests of low-level vision (length match 28/30, minimal feature view 24/25, size match 26/30 Orientation match 25/30) but was severely impaired on the object Decision Task (10/32).

Face identity matching was assessed with Benton Facial Recognition Test (BFRT) (Benton et al. 1983). EP qualified as severely impaired on the BFRT with a score

of 10 out of 27. We did not administer the Cambridge Face Memory Test (Duchaine and Nakayama 2006) as that experimental protocol included a face memory task and we preferred to minimize the probability of proactive and retroactive interference effects across memory tests.

A Dutch version of the Famous Faces task was created, consisting of 14 stimuli (7 male) from different categories, such as film, TV, music, sports, royals and politicians. EP accurately recognized only 5 of the 14 famous persons (3 male: the king and the prime minister of the Netherlands, a singer, his favorite TV presenter and an Olympic gold medalist). Post-hoc questioning revealed that EP knew all 14 celebrities by name, and he indicated that he guessed the names based on stand-out physical attributes.

Of note, EP was also impaired on object recognition tasks and is thus not a case of pure prosopagnosia. This may suggest that the OFA is affected. The imaging data indicate that the OFA is not structurally affected by the lesion, but the functional impact possibly deriving from impaired network connectivity remains unclear and was outside the scope of the present study.

Fusiform Face Area Functionality

Control participants in the imaging experiment were six age-matched healthy control subjects (three male, mean age = 46.3, age range = 39–56 years).

Procedure

EP was scanned 1 month after the strokes with a 3T whole-body scanner (Magnetom Trio, Siemens, Erlangen, Germany) equipped with a 20-element head–neck coil. A T1-weighted anatomical image (1x1x1 mm^3 isotropic) was acquired with an MPRAGE sequence (TR = 2250 ms; TE = 2.17 ms; FOV: 256x256 mm; matrix size = 256x256; slice thickness = 1 mm; flip angle = 9; Inversion time = 900 ms; GRAPPA acceleration factor = 2; pixel bandwidth = 200 Hz; echo spacing = 6.5 ms).

The localizer scan sequence consisted of a T2*-weighted gradient EPI protocol with 29 slices without gaps, covering the occipital and temporal lobes ($2 \times 2 \times 2$ mm^3 resolution, TR = 2000 ms, TE = 30 ms, flip angle = 90, matrix size = 128*128). The visual stimulation protocol consisted of a blocked design, in which 12 s stimulation blocks alternated with 12 s fixation blocks. Stimuli were back-projected onto a screen behind the participants' head and viewed through a mirror attached to the head coil at a viewing distance of ~75 cm. During the stimulation blocks, gray-scaled pictures were presented of faces, bodies, tools, and houses with a visual angle of 6.92°. A stimulus was presented for 450 ms, followed by an interstimulus interval of 580 ms. There were 5 blocks of each stimulus category. The total duration of the localizer was 540 seconds. The procedure has been reported in more detail elsewhere (Van den Stock et al. 2012).

The functional MRI data were analyzed in BrainVoyager (Brain Innovation, Maastricht, the Netherlands). Preprocessing included slice scan-time correction, 3D motion correction, spatial smoothing (FWHM = 4 mm), and temporal filtering (GLM-Fourier filtering of 2 cycles). The dataset was aligned to the anatomical image and transformed into MNI space. The four stimulus categories were convolved with the default two-gamma hemodynamic response function and entered as predictors in a GLM analysis.

Results

First, we defined the face-responsive network in the control subjects by contrasting faces with fixation in a fixed-effect analysis ($q < 0.01$, FDR-corrected). We then overlaid this network and the FFA as defined in a recent meta-analysis (Cohen et al. 2019) as well as the occipital face area (OFA), defined as a 5-mm sphere around the peak coordinate of a recent study (Schobert et al. 2018) on the structural scan and lesion of EP. This revealed that the normal face-responsive network intersected the FFA, the OFA and EP's lesion (Fig. 2). Second, we investigated the face perception network in EP, based on the contrast faces versus tools ($P < 0.005$, cluster-level corrected) (Forman et al. 1995) in ACPC and MNI-space. This revealed distributed responses in temporal cortex, including in a region that intersects the FFA (Fig. 2). We also compared faces with bodies and faces with houses, which did not reveal any significant results in the right temporal cortex.

Subsequently, we performed 4 ROI-analyses in the activation cluster that intersected with the FFA. In particular, we compared activation estimates (β-values) of faces with those of tools, houses, bodies and the combination of the latter three, that is, faces versus (tools, houses, bodies). Each of these comparisons revealed a significant results ($t(267) > 3.601$; $P < 0.001$; Fig. 3).

Configural Processing

EP was tested with a number of behavioral experiments 2 months after his stroke in two separate sessions and his performance was compared with a control group by calculating t-test scores using the mean and standard deviations (SDs) of the control group and interpreted using the t-distribution with N-1 degrees of freedom (Crawford and Howell 1998). Accuracies were calculated as the proportion of correct responses for the total score of each task and for each condition separately. Average response times from stimulus onset were calculated for the trials with correct responses. Reaction times (RT) below 150 ms were discarded. In addition, experiment-specific upper limits of RT were imposed based on visual inspection of the RT distribution of the experiment.

Inversion Effect

Control Participants

Twenty control participants from a previous normative study were selected based on age (de Gelder et al. 2015). The sample consisted of 9 men (between 47 and 56 years old, $M = 51.9$, $SD = 3.1$) and 11 women (between 50 and

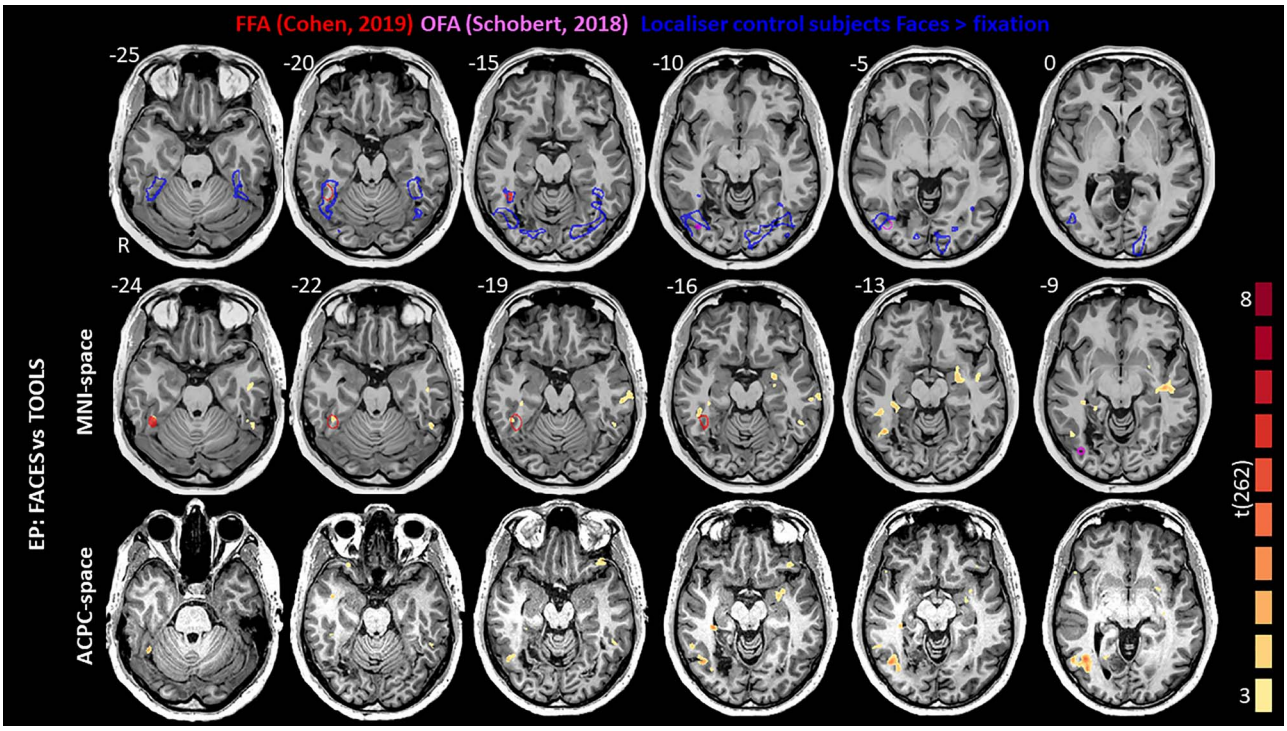

Figure 2. Lesion of EP relative to face regions. The network outlined in blue was defined based on the contrast faces versus fixation of a localizer scan in six age-matched healthy control subjects (three male, mean age = 46.3, age range = 39–56 years) following a fixed-effect analysis ($q < 0.01$, FDR-corrected). The red and pink outlines respectively display the boundaries of the FFA (Cohen et al. 2019) and OFA (Schobert et al. 2018). The top and middle row display axial slices of EP's T1-scan in MNI-space and the bottom row in ACPC-space.

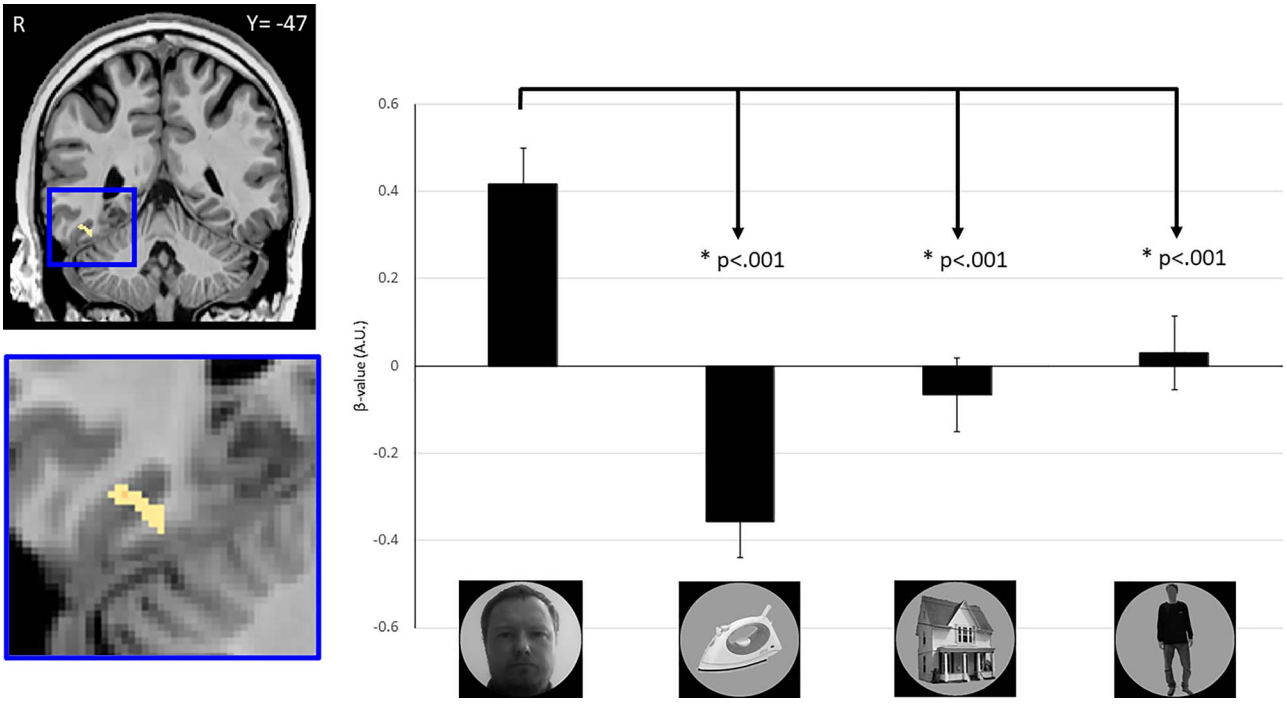

Figure 3. ROI-analyses in EP's FFA. The left column displays the location of EP's FFA on a coronal slice and the right bar-chart displays the β-values of each object category of the localizer.

56 years old, $M = 53.0$, $SD = 1.8$). There were no significant age differences between the male and female controls ($F(1,19) = 0.992$, $P = 0.332$). None of the control participants had a psychiatric or neurological history. All control subjects were right-handed.

Procedure

We used a subtest of the Facial Expressive Action Stimulus Test (FEAST), measuring face specific configural processing (de Gelder et al. 2015). The task involves matching of identity across orientation and for different stimulus

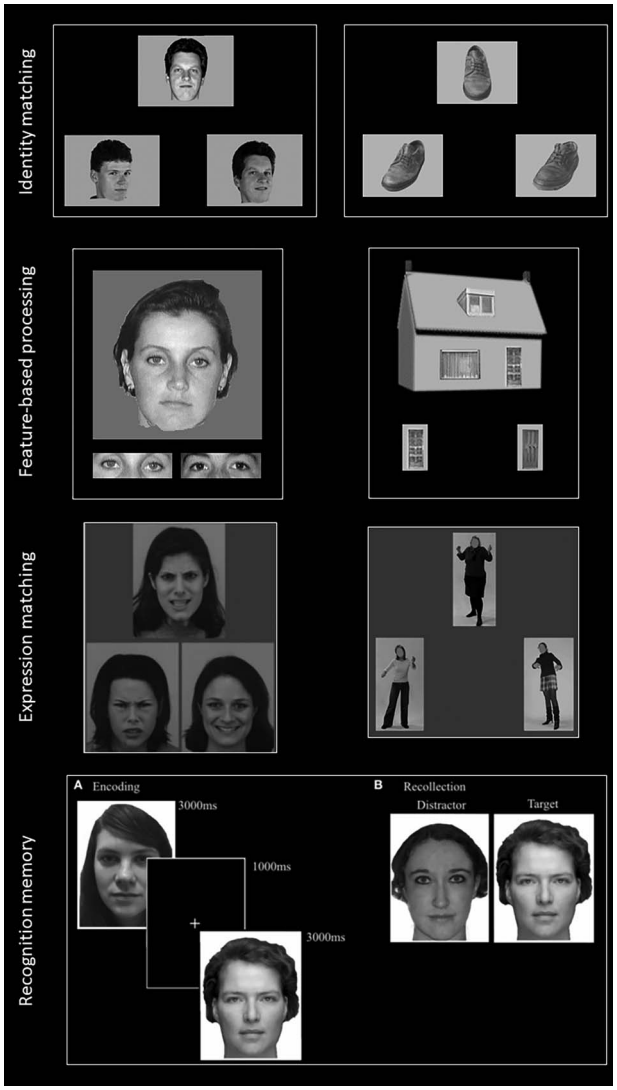

Figure 4. Stimulus examples of FEAST and BEAST subtests and schematic overview of Recognition Memory task.

categories (faces, shoes). A trial consisted of one picture presented at the top of the screen and two underneath. Presentation duration was 750 ms. Participants were instructed to indicate by a button press which of the two bottom pictures represented the same individual as the top one. All pictures in a trial always had the same orientation, that is, all three pictures in a single trial were always upright, or all three were always inverted. See Figure 4 for stimulus examples.

Results

RTs above 3000 ms were discarded. EP's accuracy was significantly lower for upright face ($T = 2.90$, $P < 0.01$) as well as for object identity matching ($T = 4.15$, $P < 0.001$) as well as for inverted object matching ($T = 2.79$, $P < 0.001$) but not for inverted face matching ($T = 1.09$). Inversion scores were calculated by subtracting upright and inverted conditions. Contrary to the normal face inversion effect displayed by the control group, EP shows a significantly different and paradoxical inversion effect ($T = 1.81$, $P < 0.05$) for faces but not for objects ($T = 1.46$). EP's RT did not significantly differ from controls on any condition (upright faces ($T = 0.12$), inverted faces $T = (0.72)$, upright objects ($T = 0.40$) or inverted objects ($T = 0.23$); Fig. 5). Also, no differences in face ($T = 1.08$) or object ($T = -0.62$) inversion scores were found.

Part-whole Effect

Control participants were the same as those for the inversion test above.

Procedure

Holistic processing was also assessed by means of a simultaneous part-to-whole matching task (de Gelder et al. 2015). A trial consists of a face or a house on top and part-stimuli (eyes or mouths, windows or doors) shown underneath. The task was to indicate which one of the bottom pictures was part of the top picture. There were 2 blocks of 32 trials per condition, resulting in a total of 8 blocks. Stimuli were presented for 750 ms. See Figure 4 for stimulus examples.

Results

EP reported that this task was too difficult for him and that he was unable to perform the task in a normal manner and testing was aborted.

Face Attributes

Facial Expressions

Control participants were the same as those for the inversion test above.

Procedure

Recognition of facial expressions was assessed with the Facial Expression Matching Task of the FEAST consisting of a match-to-sample task with one picture on top and two underneath and using five expressions (anger, disgust, fear, happy, sad and surprise). Each condition contained 10 trials (5 male) in which the target emotion was paired with a distracter. Each of the non-target emotions served twice a distracter, one of each sex, resulting in 60 trials in total. See Figure 4 for stimulus examples. The task was to match one of the two bottom pictures to the top picture according to facial expression. Exposure duration was unlimited, and instruction stressed speed and accuracy.

Results

RTs above 3000 ms were discarded. On the facial expression matching task, EP's overall score and response time was within normal limits. Furthermore, there was no significant difference on any of the emotion category condition (anger: EP = 50%; controls = 82%; disgust: EP = 60%; controls = 83%; fear: EP = 30%; controls = 52%; happy: EP = 100%; controls = 92%; sad: EP = 60%; controls = 62%; surprise: EP = 60%; controls = 81%; total: EP = 60%; controls = 75%), nor on the response time of any condition (all T's < 2.052). See Figure 6A.

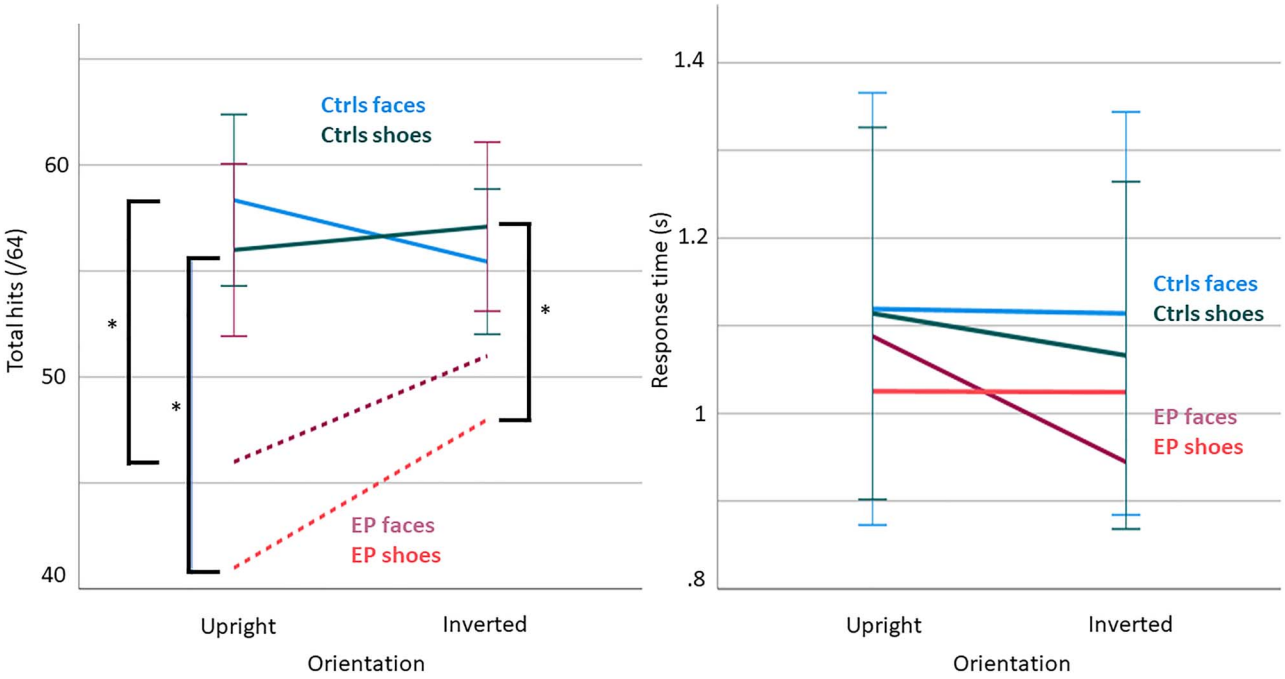

Figure 5. Mean and SD of accuracy and response times of the controls and EP on the faces and objects matching task as a function of object category and orientation. Error bars mark 1 SD, black lines mark significant differences.

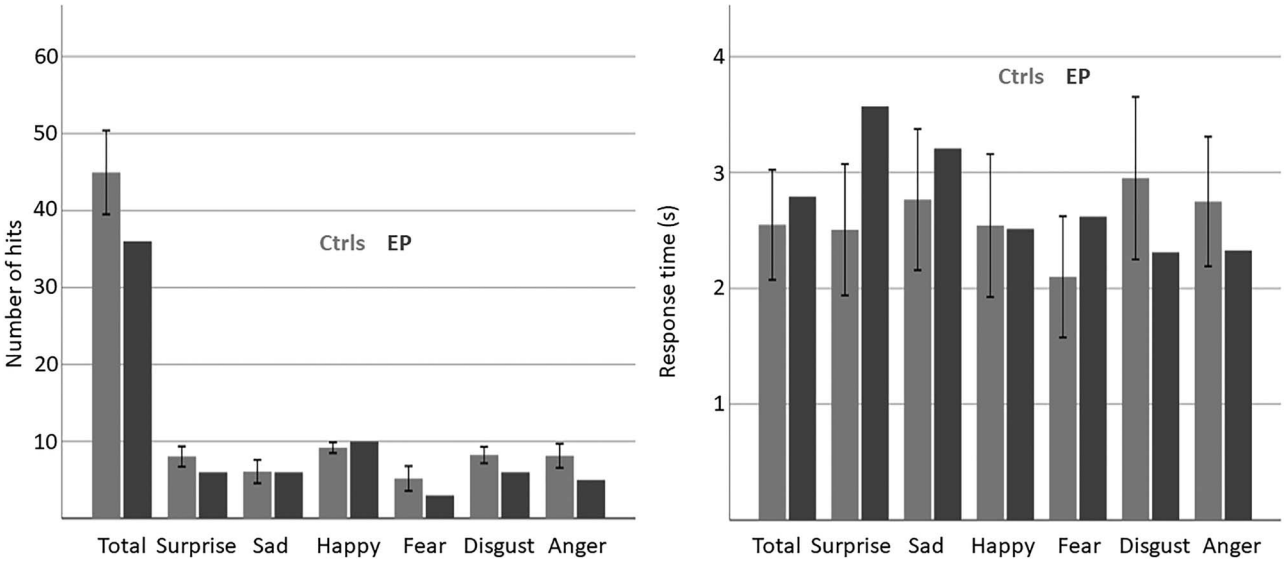

Figure 6. Mean and SD of accuracy and response times of the controls and EP on the facial emotion recognition task as a function of emotion. Error bars mark 1 SD.

Body Expressions

Control Participants

Six males (between 25 and 37 year, $M = 31.0$, $SD = 3.8$) and 7 females (between 25–58 years old, $M = 36.4$, $SD = 10.8$) were recruited from the healthy volunteer database of the lab. All control subjects were right-handed. None of the control participants had a psychiatric or neurological history. All control subjects were right-handed.

Procedure

To investigate the specificity of the facial expression recognition abilities of EP, we investigate recognition of bodily expressions by means of the Bodily Expressive Action Stimulus Test (BEAST) (de Gelder and Van den Stock 2011). A trial consisted of a picture of a face-blurred body expression presented on top with two other pictures underneath (Van den Stock et al. 2007). Participants indicated with a button press whether the left or right bottom picture expressed the same emotion as the one on top. Exposure duration was unlimited. There were 48 trials, 12 per emotion condition (half male). See Figure 4 for stimulus examples.

Results

RTs above 3000 ms were discarded. EP was normally able to recognize all emotions (Anger: $T = -0.68$, Fear:

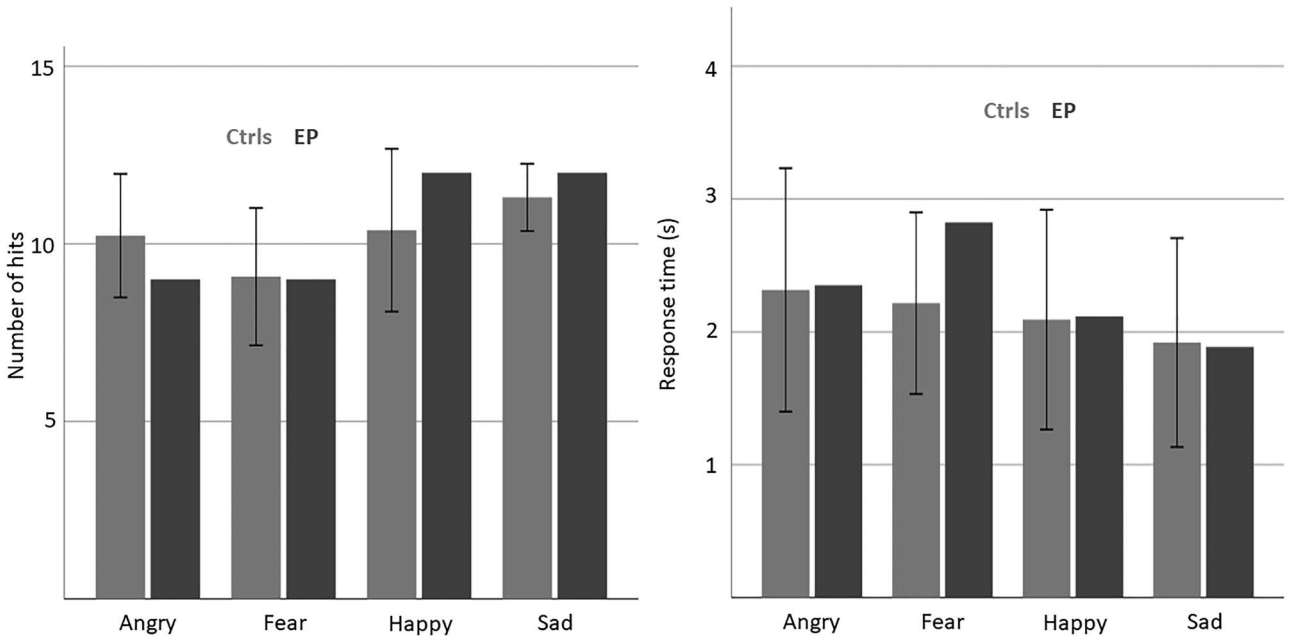

Figure 7. Mean and SD of accuracy and response times of the controls and EP on the bodily emotion recognition task as a function of emotion. Error bars mark 1 SD.

$T = -0.04$, Happy: $T = 0.68$, Sad: $T = 0.70$) and was not slower than the controls on this task (Anger: $T = 0.04$, Fear: $T = 0.85$, Happy: $T = 0.03$, Sad: $T = -0.04$). See Figure 7.

Neutral Face Identity Memory

Control participants were the same as those for the inversion test above.

Procedure

The Neutral Face Memory Task of the FEAST was used (de Gelder et al. 2015), consisting of an encoding and a recognition phase. In the encoding phase, fifty stimuli of neutral faces were randomly presented one by one for 3000 ms. The recognition phase immediately followed the encoding phase and consisted of fifty trials, each displaying two faces of which only one was presented in the encoding phase. Participants were instructed to indicate the face they recognized. See Figure 4 for stimulus examples and schematic overview of procedure.

Results

RTs above 5000 ms were discarded

EP was significantly impaired on recognition memory for neutral face identity, with an accuracy of 54% significantly lower than the control accuracy of 80% ($T = -2.79$, $P < 0.01$). In contrast, he was not significantly slower ($T = 0.04$). See Figure 8.

Emotional Face Identity Memory

Control participants were the same as those for the inversion test above.

Procedure

Recognition memory for emotional faces was assessed using the Emotional Face Memory Task of the FEAST (de Gelder et al. 2015). It has a similar design as the Neutral Face Memory Task, but contains 48 trials displaying fearful ($N = 16$), sad ($N = 16$) and happy ($N = 16$) faces instead of neutral faces.

Results

RTs above 5000 ms were discarded. EP's performance on recognition memory for emotional face identity was deficient, with a total accuracy of 48% ($T = -3.52$, $P < 0.005$). Furthermore, his performance on each of the emotion conditions was deficient (Fear: $T = -2.33$, $P < 0.05$, Happy: $T = -2.79$, $P < 0.05$, Sad: $T = -4.19$, $P < 0.001$). In contrast, EP was not significantly slower on any of the conditions (total: $T = 0.72$, Fear: $T = 0.77$, Happy: $T = 1.39$, Sad: $T = -0.58$). See Figure 8.

Discussion

With this study of a new case of acquired prosopagnosia with structurally intact FFA and OFA, but with bilateral damage in inferior occipito-temporal cortex, we investigated whether damage to the face-network affects the face-selective response of the FFA and how this is reflected at the behavioral level in face identity and facial expression perception.

First, we found that an area corresponding to the FFA still shows a face-selective response. The selectivity of this response was consistent, as we observed a stronger response for faces compared to each of three other stimulus categories, that is, tools, houses and bodies, as well as to the pooled control conditions. This indicates that

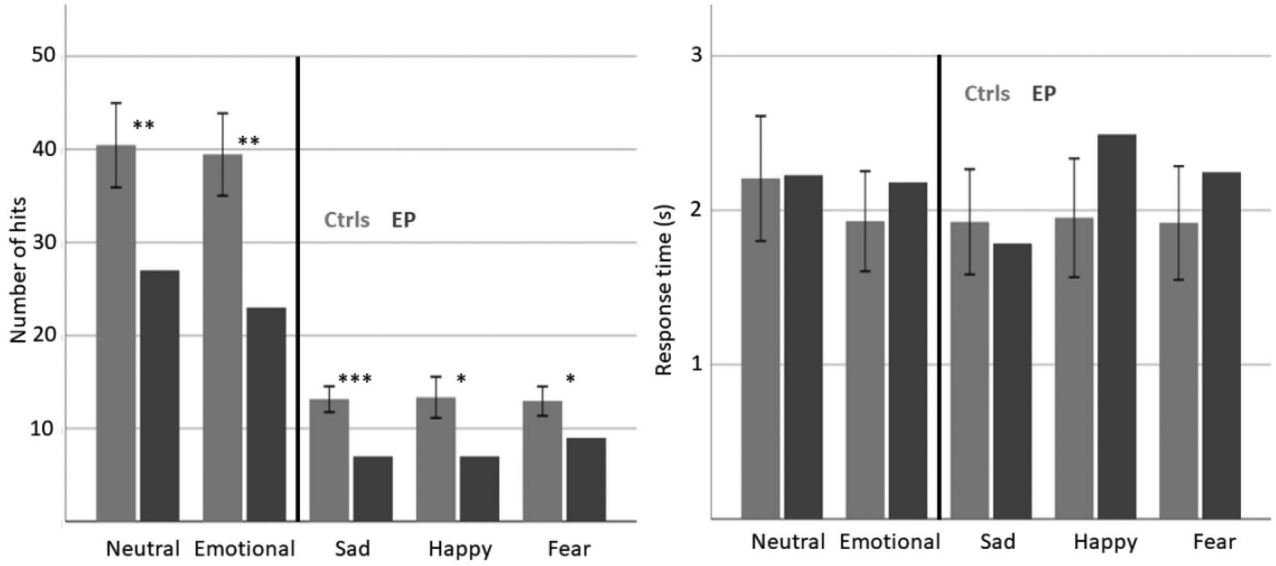

Figure 8. Mean and SD of accuracy and response times of the controls and EP on the face identity recognition memory task as a function of emotion. Error bars mark 1 SD. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

despite the structural damage to non-FFA and non-OFA regions of the face network, the face-selective function properties of EP's FFA is preserved. This is a remarkable finding, considering the extent of the lesion posterior to the FFA, presumably significantly affecting the ventral visual feed-forward stream into the FFA and thus at least partly de-afferenting the FFA. We can only speculate whether the preserved face-selective function of EP's FFA is sustained by the part of the ventral visual stream that has remained structurally intact, or by functional plasticity of the face-selective circuit, or by a combination of both. Our results thus indicate that prosopagnosia can occur with structural and functional integrity of the FFA and this is consistent with 17 out of 44 cases of acquired prosopagnosia reviewed recently (Cohen et al. 2019). Our study extends that information by now providing evidence that the FFA has retained its face selectivity. We propose that the preserved functionality of the FFA in EP indicates that face template-like computations that can still take place here corresponds to processes of face detection and face versus non-face discrimination. We previously indicated the importance of a face detection component in the early stages of face processing (de Gelder and Rouw 2001) based on the fact that often prosopagnosic subjects have no difficulty detecting faces in a noise pattern or deciding whether a stimulus is a face even from very brief exposures like 50 msec (de Gelder and Rouw 2000b). However, although we identified a face specific area overlapping the FFA region, it cannot be ruled out that this area is indeed the FFA of EP's pre-stroke healthy brain. It may respond now to faces more than to other stimuli, but this does not mean that the current region is identical to his FFA prior to the lesion. Indeed, there is a significant amount of interindividual variability in the FFA and it cannot be excluded that the EP's FFA was originally damaged and the current activity is a residual response from an adjacent area. As we have no data of EP prior to the strokes, this issue cannot be resolved.

Secondly, we observed that EP's face configuration processing is impaired presumably explaining his failure at face identification and more specifically, at performing the two configuration tests. In line with many other APs, EP was impaired in recognizing identity from upright but not from inverted faces. Similarly, he was unable to successfully perform a part-to-whole facial identity matching task. These findings convergingly indicate that his configural processing is disrupted. Furthermore, in EP configuration computing was specifically lost for faces and not for objects. This specificity indicates an interdependence between category selectivity and configurational computations, specifically for the case of faces. Impaired configurational processing for faces has often been associated with damage to the fusiform gyrus, especially the FFA (e.g. Barton et al. 2002; Joubert et al. 2003). The present findings challenge this hypothesis, as the face-selectivity of the FFA is preserved in EP, yet he showes a face-selective deficit in configuration processing.

The face-object inversion task that EP performed was the topic of an fMRI study in neurotypical participants (Watson et al. 2016) and the results speak directly to the pattern of EP. Upright versus inverted faces elicited activity in the right fusiform gyrus while upright versus inverted objects showed higher activation in the middle occipital gyrus. These combined findings indicate that the face-selective functionality of the FFA is not sufficient to sustain further computing of the overall configuration of the face such that a representation is generated as pictured in the core-extended face models (Grill-Spector et al. 2018).

Of note, the holistic issue relates to face-like non-face stimuli, for example, Arcimboldo portraits (Steeves et al. 2006; Rivest et al. 2009; Busigny et al. 2010), which are

composed of single elements, for example, food, which on their own do not trigger face processing. Yet, the studies show that right occipitotemporal lesions do not affect this type of face processing, while left-sided lesions typically result in a deficit (Pavlova et al. 2015; Pavlova, Heiz, et al. 2016a; Pavlova, Mayer, et al. 2016b; Pavlova, Erb, et al. 2017a; Pavlova, Guerreschi, et al. 2017b; Pavlova, Galli, et al. 2018a; Pavlova, Heiz, et al. 2018b; Kubon et al. 2021).

Evidence of intact face detection discussed in the first sections here, contrasts with impaired configuration processes for facial identity. Taken together we see here that face detection involves some configuration or face template processing of a kind that does not need the connectivity of the FFA with other areas, while configuration processing for identity processing apparently does. On the other hand, the face selectivity of the FFA as seen here in the evidence for intact face detection may be supported by other, intact brain areas that are also face selective and outside the face perception network like for example the amygdala (Taubert et al. 2018).

Third, EPs' overall performance of facial expression recognition was comparable to that of controls. Spared emotion recognition ability in combination with impaired identity recognition suggests separate systems and indicate that configuration processing for expression recognition may rely on different resources than configuration computation used in identity recognition. This mixed pattern is often found in APs with damage to the occipital or occipitotemporal regions (Bruyer et al. 1983; De Renzi and di Pellegrino 1998; Mattson et al. 2000; Riddoch et al. 2008; Fox et al. 2011) and is consistent with studies showing that in the intact brain FFA activity is influenced by facial expression (de Gelder et al. 2003; Van den Stock et al. 2008; Fox et al. 2009; Xu and Biederman 2010; Kawasaki et al. 2012; Harry et al. 2013). In contrast, anterior temporal lobe or parietal lobe damage (Humphreys et al. 1993; Stephan et al. 2006; Humphreys et al. 2007), or damage to the OFA (Steeves et al. 2006) seems to cause more problems in emotion recognition (but see, Fox et al. 2011). We also probed recognition of body expressions as a selectivity control for a facial expression recognition deficit. As the latter was not observed, the intact body expression recognition performance corroborates his intact emotion recognition abilities in configurally processed stimulus classes.

Fourth, EP was impaired on recognition memory for facial identity. His deficit was evident for both neutral and emotional faces and extends his identity recognition deficit. Very few AP cases have been tested on memory for identity with facial expressions and the results are inconclusive. It has been previously shown that emotion, especially fear, can influence identity processing (Peelen et al. 2009; Van den Stock and de Gelder 2014). EPs' pattern of results suggests that he is slightly better able to remember identities with fearful rather than happy or sad expressions, even though his overall performance is still impaired.

Overall, the pattern of impaired configural processing for facial identity with normal facial expression recognition and configural non-face processing, supports the notion that configural perception is a general ability but that it can be locked-in for the face category by the requirements of face specificity when the task is identity perception. It is is released for expression perception and for object perception, processes that also normally involve configuration perception (Calder et al. 2000; Vuilleumier et al. 2001; de Gelder et al. 2003; Phelps 2004; Durand et al. 2007; Garrido et al. 2012; Tanaka et al. 2012). The relation between face identity and expression continues to be a matter of debate as much in models of intact face perceptions as for understanding prosopagnosia. The early models distinguished two separate systems (Bruce and Young 1986; Haxby et al. 2000), but still make the extended system dependent on the core system as long as this is viewed as the entry level stage of face perception. More recently, many studies found evidence for interactions between identity and expression perception suggesting shared mechanisms or shared representations (Calder and Young 2005; Calder 2011; Van den Stock and de Gelder 2012, 2014; Fisher et al. 2016).

Some limitations of the present study should be noted. Our localizer scan did not include a low-level control condition for the faces, for example, scrambled faces (Rossion et al. 2012). However, there is a large body of evidence indicating that the face-response in the FFA cannot be explained by low-level features. First, the FFA response is similar for a variety of face stimuli that differ substantially in their low-level features, including front and profile face views (Tong et al. 2000), line drawings (Spiridon and Kanwisher 2002), animal faces (Tong et al. 2000) and "Mooney faces." Second, the FFA response to upright faces is stronger than to inverted faces, despite identical low-level features like luminance and spatial frequencies (Kanwisher et al. 1998; Rhodes et al. 2004). Third, in bistable stimulus configurations like binocular rivalry paradigms and Rubin face-vase illusion, the FFA response is increased when the conscious perception consists of a face, compared to a rivaling object category. Yet, the retinal images are identical (Tong et al. 1998; Hasson et al. 2001; Andrews et al. 2002; Pasley et al. 2004; Williams et al. 2004). The second limitation relates to the focus of the study. The anatomical topography of EP's lesion inspired a strong anatomical focus on the FFA. While this is the primary region associated with face processing, the functional impact on other face regions like the OFA, STS, amygdala, inferior frontal gyrus and anterior temporal lobe fell outside the scope of the present study and may be of interest for future studies.

In conclusion, the present results document a new case of AP with lesions in the face perception network, but with structurally intact OFA and FFA, which also shows a face-selective response. Behaviourally, EP showed impaired configural processing for facial identity, but not for other stimulus categories and not

for expression recognition. These findings challenge a critical role of the FFA for face identity processing and support a domain-specific account of configural processing.

Notes

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