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Research report

Beyond the core face-processing network: Intracerebral stimulation of a face-selective area in the right anterior fusiform gyrus elicits transient prosopagnosia

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ABSTRACT

According to neuropsychological evidence, a distributed network of regions of the ventral visual pathway – from the lateral occipital cortex to the temporal pole – supports face recognition. However, functional magnetic resonance imaging (fMRI) studies have generally confined ventral face-selective areas to the posterior section of the occipito-temporal cortex, i.e., the inferior occipital gyrus occipital face area (OFA) and the posterior and middle fusiform gyrus fusiform face area (FFA). There is recent evidence that intracranial electrical stimulation of these areas in the right hemisphere elicits face matching and recognition impairments (i.e., prosopagnosia) as well as perceptual face distortions. Here we report a case of transient inability to recognize faces following electrical stimulation of the right anterior fusiform gyrus, in a region located anteriorly to the FFA. There was no perceptual face distortion reported during stimulation. Although no fMRI face-selective responses were found in this region due to a severe signal drop-out as in previous studies, intracerebral face-selective event-related potentials and gamma range electrophysiological responses were found at the critical site of stimulation. These results point to a causal role in face recognition of the right anterior fusiform gyrus and more generally of face-selective areas located beyond the "core" face-processing network in the right ventral temporal cortex. It also illustrates the diagnostic value of intracerebral electrophysiological recordings and stimulation in understanding the neural basis of face recognition and visual recognition in general.

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1. Introduction

The ability to recognize people by their face is an extremely important function of the human brain, critical for social interactions. The neural basis of this function has been defined by studies of patients with face recognition impairment following brain damage – prosopagnosia – (Bodamer, 1947), which point to a large territory of the ventral occipito-temporal cortex, from the lateral occipital cortex to the temporal pole, with a right hemisphere advantage (Barton, 2008; Busigny et al., 2014a; Hécaen & Angelergues, 1962; Meadows, 1974; Rossion et al., 2003a; Sergent & Signoret, 1992; see Rossion, 2014 for a review). Early neuroimaging studies using positron emission tomography (PET) as well as intracranial recordings by means of subdural grids of electrodes electrocorticography (ECOG) have also shown larger responses to faces than objects (i.e., "face-selective" responses) across the entire ventral occipito-temporal cortex, again with a right hemisphere advantage (Sergent, Ohta, & MacDonald, 1992 for PET; Allison, McCarthy, Nobre, Puce, & Belger, 1994 and Allison, Puce, Spencer, & McCarthy, 1999 for ECOG).

Subsequent studies using functional magnetic resonance imaging (fMRI) have generally confined face-selective areas to the posterior half of the ventral occipito-temporal cortex, namely in the inferior occipital gyrus [occipital face area (OFA), Gauthier et al., 2000] and in the posterior and middle fusiform gyrus [fusiform face area (FFA), Kanwisher, McDermott, & Chun, 1997; Puce, Allison, Gore, & McCarthy, 1995]. Together with a face-selective region in the posterior part of the superior temporal sulcus (pSTS), these areas have been defined as the "core" network for face perception (Atkinson & Adolphs, 2011; Calder & Young, 2005; Haxby, Hoffman, & Gobbini, 2000; Ishai, 2008; Rossion, 2008; Weiner & Grill-Spector, 2010). Moreover, transcranial magnetic stimulation (TMS) applied on the scalp, and intracranial electrical stimulation, have shown that areas of the core network play a causal role in face recognition (Pitcher, Walsh, Yovel, & Duchaine, 2007; Solomon-Harris, Mullin, & Steeves, 2013 for TMS studies of the OFA; Jonas et al., 2012, 2014; Parvizi et al., 2012 for intracranial electrical stimulation studies). Jonas et al. (2012) reported a case of transient prosopagnosia by electrically stimulating the right OFA of an epileptic patient implanted with depth electrodes. Parvizi et al. (2012) reported a distortion of a clinician's face during electrical stimulation of the cortical surface over the right FFA (see also Rangarajan et al., 2014).

Most recently, fMRI studies have also reported ventral face-selective regions anterior to the FFA, up to the temporal pole (e.g., Avidan et al., 2014; Nasr & Tootell, 2012; Rajimehr, Young, & Tootell, 2009; Rossion, Hanseeuw, & Dricot, 2012; Tsao, Moeller, & Freiwald, 2008; for a recent review, see Collins & Olson, 2014). Unfortunately, due to large hemodynamic signal drop-outs caused by magnetic susceptibility artifacts (Axelrod & Yovel, 2013; Ojemann et al., 1997), fMRI studies are limited in their understanding of the function(s) of the anterior ventral temporal face-selective areas, in particular in the anterior part of the fusiform gyrus (e.g., Fig. S7 in Rajimehr et al., 2009; Fig. S7 in Tsao et al., 2008). Moreover, unlike the OFA and pSTS, the function of these ventral regions cannot be disrupted by TMS during face recognition. Hence, aside from the association of lesions in the right anterior temporal lobe with acquired prosopagnosia (e.g., Busigny et al., 2014a) and reduced cortical volume of the anterior part of the fusiform gyrus in low performers at face recognition (i.e., "congenital prosopagnosia", Behrmann, Avidan, Gao, & Black, 2007), the causal role of anterior ventral temporal regions in this function remains largely unknown.

Here we report a novel case of transient prosopagnosia following electrical stimulation of a face-selective region of the right ventral temporal cortex located anteriorly to the FFA. As in previous studies of our group (Jonas et al., 2012, 2014), this epileptic patient (CD) was implanted with depth intracerebral electrodes [stereotactic electroencephalography (SEEG), Talairach & Bancaud, 1973; e.g., Barbeau et al., 2008; Halgren et al., 1994]. While performing electrical stimulation of the patient's right anterior fusiform gyrus (anterior FG), we observed her transient inability to recognize famous face photographs. Intracerebral electrophysiological face-selective responses were recorded at the critical site of stimulation. A subsequent fMRI examination showed that the critical stimulation site was located anteriorly to the right FFA, extending further the causal role of face-selective areas to anterior ventro-temporal regions beyond the core face-processing network.

2. Materials and methods

2.1. Case description

The patient was a 44-year-old woman (CD) who had medically intractable left temporal epilepsy related to a left temporal lobe schizencephaly. She never complained of face recognition difficulties in everyday life or during and after epileptic seizures.

She was right-handed as attested by the Edinburgh Handedness Inventory (Oldfield, 1971) and also by intracerebral electrical stimulations performed during the SEEG exploration (stimulations in the left FG elicited impairments in naming and reading, showing unambiguously the left hemispheric language dominance). The SEEG exploration took place in June 2011. SEEG exploration delineated the seizure onset zone in the left ventral temporal cortex. CD was contraindicated to conventional resection and she did not have surgery eventually. The face processing behavioral tests and the neuroimaging recordings took place in April and May 2014. CD gave written consent to participate in the experimental procedures, which were part of the clinical investigation.

2.2. Neuropsychological assessment

2.2.1. General assessment

Patient CD showed a general intelligence in the lower range (full-scale IQ of 70) with verbal-performance IQ discrepancy (performance score > verbal score). She was impaired in object naming and verbal fluency. This impairment in language functions is consistent with the localization of the brain lesion and the epileptic focus in the left temporal lobe. Importantly, CD showed normal basic visual perception attested by the

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Visual Object and Space Perception Battery (VOSP). The results of this neuropsychological assessment are summarized in Table 1.

2.2.2. *Face perception and memory*

We conducted a series of stringent behavioral tests to assess CD's face/object perception and memory. Six control participants (age-, sex- and education level-matched controls, not matched in IQ) performed the same tests. To compare the results of CD to the control participants, we used the modified *t*-test of Crawford–Howell for single-case studies (Crawford & Howell, 1998) with a p value of <.05 considered as statistically significant. These tests included: (1) individual discrimination of unfamiliar categories: individual face matching (Benton Face Recognition Test: BFRT, Benton, Sivan, Hamsher, Varney, & Spreen, 1983) and individual face and car matching at upright and inverted orientations (experiment 22 in Busigny, Joubert, Felician, Ceccaldi, & Rossion, 2010); (2) visual memory: encoding followed by an old/new forced choice decision with faces (experiment 3 in Busigny et al., 2010) and on the same task with bird pictures, using the same parameters as for faces; (3) a famous face recognition test for French celebrities (cropped faces, CELEB test, Busigny et al., 2014b).

The results of these tests are shown in Table 2. Patient CD was in the normal range at individualizing unfamiliar faces. She was in the normal range at the BFRT and at matching upright and inverted faces. Her decrease of performance for inverted compared to upright faces (accuracy: 86.6% *vs* 72.2%; reaction times: 1553 msec *vs* 1869 msec) was also in the normal range ($t = .62$, $p = .56$ and $t = .99$, $p = .37$ respectively, revised standardized difference test, Crawford & Garthwaite, 2005). However, she scored below normal controls at the old/new test for faces and non-face objects (birds), although her performance at memorizing faces was well above chance level (73.3%). She was also below normal controls at recognizing famous faces [CELEB test, Face Recognition Index (FRI)] and at naming famous faces [CELEB test, Name Access Index (NAI)].

In summary, patient CD had no impairment at perceiving faces but she was below normal controls at memorizing unfamiliar faces, and at recognizing and naming famous faces. Such difficulties are often found in patients with temporal lobe epilepsy (Glosser, Salvucci, & Chiaravalloti, 2003). Nevertheless, we acknowledge that this is a factor to take into account for the experimentation (i.e., the identity of the famous faces selected) and the interpretation of the behavioral tests with faces performed during intracerebral stimulation (see Discussion section).

Table 1 – General neuropsychological assessment of patient CD.

	Score
IQ	
WAIS-R	
Verbal IQ	64
Performance IQ	80
Full-scale IQ	70
Memory	
Immediate memory/Working memory	
Forward span	5
Backward span	4
Grober & Buschke 16 items	
Encoding	16/16
Immediate free recall	9-9-12/16
Immediate total recall	15-16-16/16
Recognition	16
Delayed free recall	11/16
Delayed total recall	16/16
Basic visual perception	
Visual Object and Space Perception Battery (VOSP)	
Screening test	19/20
Incomplete letters (test 1)	20/20
Silhouettes (test 2)	20/30
Dot counting (test 5)	10/10
Position discrimination (test 6)	17/20
Number location (test 7)	10/10
Language	
Verbal fluency in 2 min	
Semantic (letter R)	20
Phonological ("fruit" category)	12[a]
Naming (DO 80)	65/80[a]
Reading words	20/20

[a] Indicates impaired scores.

2.3. *Stereotactic placement of intracerebral electrodes*

Intra-cerebral electrodes (Dixi Medical, Besançon, France) were stereotactically implanted in the patient's brain in order to delineate the seizure onset zone (Talairach & Bancaud, 1973). The sites of electrode implantation were determined based on non-invasive data collected during an earlier phase of the investigation. Each intracerebral electrode consists in a cylinder of .8 mm diameter and contains 5–18 contiguous contacts of 2 mm in length separated by 1.5 mm from edge to edge. A few days before surgery, a non-stereotactic T1 weighted MRI with gadolinium was carried out and imported into a computer-assisted software (iPlan Stereotaxy, Brainlab, Germany). Each electrode trajectory was then determined according to the investigation planning with careful avoidance of vascular structures. The day of surgery, after induction of general anesthesia, the stereotactic frame (Leksell G-frame, Elekta, Sweden) was positioned on the patient's head. A stereotactic CT-scan was then carried out and fused to the pre-operative non-stereotactic MRI. Stereotactic coordinates were then calculated for each trajectory. A post-operative non-stereotactic CT-scan was carried out and fused with a T1-weighted MRI to determine the exact position of each electrode.

Nine electrodes were placed in the left hemisphere targeting the occipito-temporal cortex. Two electrodes were also placed in the right hemisphere, targeting the right ventral occipito-temporal cortex. Electrode F (containing 12 contacts) explored the anterior FG and the adjacent occipito-temporal sulcus (OTS). The border between the anterior and posterior FG was defined as the most posterior temporal lobe slice where the hippocampus was visible (e.g., Onitsuka et al., 2003). Electrode O (containing 12 contacts) explored the ventral occipital cortex (inferior bank of the calcarine sulcus and inferior occipital gyrus).

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Table 2 – Performances of CD and 6 control participants in neuropsychological tests on face/object perception and memory (Acc: accuracy; RT: reaction times in ms; BFRT: Benton Face Recognition Test; FRI: Face Recognition Index; NAI: Name Access Index).

		Patient CD	Normal controls ($n = 6$)	t-test (Crawford–Howell)
BFRT	Acc	40/54	45.4/54 ± 2.7	$t = 1.808$, $p = .065$
	RT	445[a]	254 ± 77.6	**$t = 2.278$, $p = .036$**
Face matching (upright and inverted)	Acc upright	86.1%	93.3% ± 5	$t = 1.326$, $p = .121$
	Acc inverted	72.2%	80% ± 10	$t = .716$, $p = .253$
	RT upright	1553	1292 ± 229	$t = 1.055$, $p = .17$
	RT inverted	1869	1496 ± 469	$t = .738$, $p = .247$
Car matching (upright and inverted)	Acc upright	94.4%	95% ± 3.6	$t = .144$, $p = .446$
	Acc inverted	86.1%[a]	95.6% ± 3.7	**$t = 2.365$, $p = .032$**
	RT upright	1528[a]	1086 ± 185	**$t = 2.212$, $p = .039$**
	RT inverted	1752[a]	1134 ± 234	**$t = 2.261$, $p = .037$**
Old/New face	Acc	73.3%[a]	90% ± 4.7	**$t = 3.276$, $p = .011$**
	RT	1624	1763 ± 513	$t = .250$, $p = .406$
Old/New bird	Acc	50%[a]	87.8% ± 8.4	**$t = 4.183$, $p = .004$**
	RT	2168	1742 ± 557	$t = .709$, $p = .255$
CELEB test	FRI	63.5[a]	90.8 ± 8.7	**$t = 2.909$, $p = .017$**
	NAI	53.1[a]	87.3 ± 10.4	**$t = 3.053$, $p = .014$**

[a] Indicates impaired scores compared to matched normal controls ($p < .05$).

2.4. *Intracerebral electrical stimulations*

Intracerebral electrical stimulations targeting the right ventral occipito-temporal cortex (contacts of electrodes F and O) were carried out while the patient performed famous face and object recognition tasks and a face versus object categorization task (Table 3). These stimulations were applied between two contiguous contacts along one common electrode and performed at 50 Hz during 5 sec or 10 sec at intensities ranging from .8 to 1.2 mA (usual stimulation settings in SEEG). CD was not aware of the stimulation onset and termination, the stimulation site and the nature of the impairments that could be potentially elicited.

Table 3 – Number of electrical stimulations performed at each stimulation site and type of task asked. The corresponding number of stimulations that evoked a transient impairment is indicated in brackets (aFG: anterior fusiform gyrus; CoS: collateral sulcus; CS: calcarine sulcus; IOG: inferior occipital gyrus; ITG: inferior temporal gyrus; ITS: inferior temporal sulcus; OTS: occipito-temporal sulcus; WM: white matter).

Stimulation site	Cognitive tasks		
	Famous face recognition	Object recognition	Face/object categorization
F1–F2 (CoS-aFG)	1 (0)		
F3–F4 (aFG)	5 (5)	2 (0)	3 (0)
F4–F5 (aFG-OTS)	2 (2)	1 (0)	
F5–F6 (OTS)	1 (1)		
F7–F8 (ITS)	1 (0)		
F8–F9 (ITG)	1 (0)		
O1–O2 (CS)	1 (0)		
O2–O3 (CS)	1 (0)		
O3–O4 (CS)	1 (0)		
O5–O6 (CS)	1 (0)		
O6–O7 (CS)	1 (0)		
O7–O8 (WM)	1 (0)		
O9–O10 (IOG)	1 (0)		

2.4.1. *Famous face and object recognition task*

Stimulations were carried out during recognition of sets of photographs of the same category presented one by one (famous faces with all external features or common objects). The patient had to name each photograph in turn. She had to recognize several photographs, before, during and after the stimulation (Fig. 1A, Table 4). For each set, the stimulation was triggered randomly during the presentation of one of the photographs. The stimulation was triggered manually, around .5–1 sec before the visual presentation and the current was delivered throughout the entire duration of the visual presentation. Because of a limited time of testing due to the clinical context, we first screened all the contacts located in the right hemisphere using one stimulation per site (electrodes F and O). Next, we studied more extensively the relevant contacts evoking face recognition impairment by performing additional electrical stimulations on these sites. Thirteen famous faces that CD easily recognized and named prior to the stimulation procedure were selected. The number of stimulations was well above the number of face photographs used, so that the same faces were repeated across stimulations. In total the patient was presented with 51 photographs of faces, 22 during electrical stimulation, 19 before and 10 after. CD was also presented with 16 different objects (no repetition), 6 during the time of the stimulation, 4 before and 6 after.

Immediately after 3 stimulations of one site in the anterior FG (contacts F3–F4), CD was asked to recall the faces that were presented during the stimulation procedure (recall task, Fig. 2B). She was presented again with the faces presented during the stimulation procedure along with distractors (for 2 stimulations) and was asked to indicate verbally which of these faces she saw a moment ago.

2.4.2. *Face/object categorization task*

During stimulations of one site in the right anterior FG (F3–F4, Table 3), CD was presented alternatively with photographs of faces and objects (the same as in the recognition task) and was

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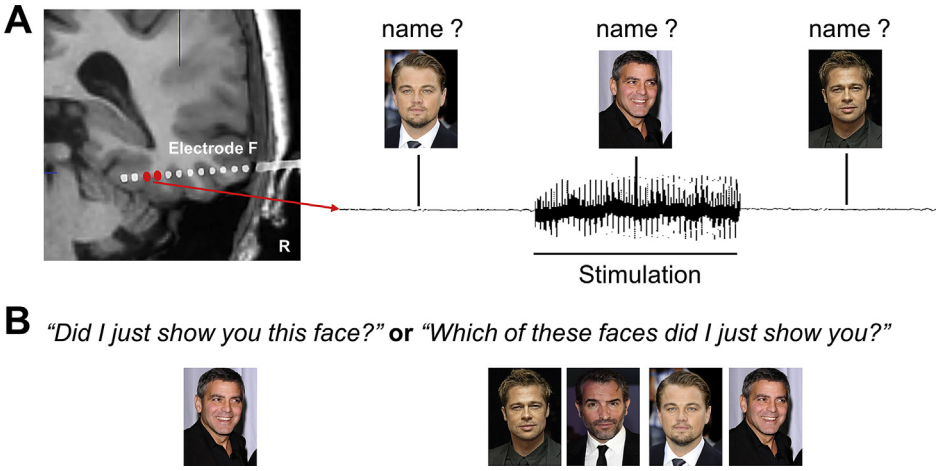

Fig. 1 – Schematic representation of the stimulation procedure for the famous face recognition task and the recall task. A. In the famous face recognition task, the patient CD had to recognize several photographs of famous faces before, during and after the electrical stimulation of 2 contiguous electrode contacts (here located in the anterior FG). She was presented mainly with famous faces of French politicians, actors, singers, etc. but famous faces of internationally renowned celebrities are showed here for illustration. B. When tested, after the stimulation procedure, CD was presented with the faces again as well as faces not presented during the stimulation (face distractors) and she was asked to indicate the faces that were presented before (recall task).

Table 4 – Details of electrical stimulation during famous face recognition: stimulation site, stimulation parameters (intensity, duration), performance (before, during and after stimulation) and transcripts of the patient responses during stimulation. The anatomical locations of the stimulation sites are indicated in Table 3.

Stimulation site	Stimulation parameters	Performance	Patient responses during stimulation
F1–F2	1 mA, 5sec	Before: 1/1 During: 1/1	Named the face
F3–F4	1 mA, 5sec	During: 0/1	Remained silent
F3–F4	1 mA, 5sec	During: 0/1	"Damn"
F3–F4	1 mA, 10sec	Before: 3/3 During: 0/1	"Damn" (see Video S3)
F3–F4	1 mA, 10sec	Before: 3/3 During: 0/1 After: 3/5	"Why am I blocked?" (see Video S2)
F3–F4	1 mA, 10sec	During: 0/1	"It's a man, he is smiling"
F4–F5	1 mA, 5sec	During: 0/1	"I'm blanking"
F4–F5	1 mA, 5sec	Before: 3/3 During: 0/1	"Damn" (see Video S1)
F5–F6	1 mA, 5sec	Before: 1/1 During: 0/1 After: 1/1	"Er"
F7–F8	1.2 mA, 5sec	During: 1/1	Named the face
F8–F9	1.2 mA, 5sec	During: 1/1	Named the face
O1–O2	1 mA, 5sec	During: 2/2 After: 4/4	Named the 2 faces
O2–O3	.8 mA, 5sec	During: 1/1	Named the face
O3–O4	.8 mA, 5sec	Before: 2/2 During: 2/2	Named the 2 faces
O4–O5	.8 mA, 5sec	Before: 1/1 During: 1/1	Named the face
O5–O6	.8 mA, 5sec	Before: 2/2 During: 1/1	Named the face
O6–O7	.8 mA, 5sec	Before: 1/1 During: 1/1	Named the face
O7–O8	.8 mA, 5sec	Before: 2/2 During: 2/2	Named the 2 faces
O9–O10	1.2 mA, 5sec	During: 1/1	Named the face

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asked to tell whether the photograph represented a face or an object. In total, she was presented with 23 stimuli (11 faces, 12 objects) with 17 of these stimuli presented during the time of stimulation (9 faces, 8 objects) and 6 before or after stimulation (3 faces, 3 objects).

2.5. *Face-selectivity: intracerebral ERP and gamma activity*

2.5.1. *Procedure*

The material consisted of 60 grayscale pictures of faces and of 60 grayscale pictures of objects. All faces showed a frontal view with a neutral background and neutral or mildly positive expressions. The patient seated in a hospital bed facing a computer screen placed 70 cm from her face. Stimuli were presented on the center of the screen using Bq-Evoque v1.0.3 software (Micromed, Italy). Stimulus duration was 396 msec. Interstimulus interval was filled by a black screen and varied randomly between 2000 and 3000 msec. The task consisted of determining whether the presented stimulus was a face or an object (by pressing keyboard buttons). The patient performed 2 blocks of 120 trials (60 faces and 60 objects in each block, randomized). The signal was recorded at a 512 kHz sampling rate on a 128 channels amplifier (2 SD LTM 64 Headbox; Micromed, Italy). The reference electrode was an intracerebral contact located in the white matter (left parietal lobe).

2.5.2. *ERP analysis*

Off-line processing of intracerebral EEG was computed using Letswave 5 (http://nocions.webnode.com/letswave/) and MATLAB v7.9 (The Mathworks, Inc.). Epochs were created beginning 200 msec before stimulus onset and lasting until 1000 msec post-stimulus. A baseline correction was applied between −200 msec and 0 msec. Averaging was computed separately for faces and objects stimuli. Amplitude differences between faces and objects ERPs were assessed with a two-tailed *t*-test ($p < .01$, 10 consecutive milliseconds at least).

2.5.3. *Gamma-ERSP analysis*

Event-related spectral perturbations (ERSP) were computed using Letswave 5 and MATLAB v7.9. Variation in signal amplitude as a function of time and frequency was estimated by a Morlet wavelet transform on each single trial from frequencies of 1–160 Hz, in 160 steps. Analyses concentrated on the high frequency broadband range (gamma: 30–160 Hz; Lachaux et al., 2005; Parvizi et al., 2012; Sato et al., 2014; Vidal et al., 2010). Broadband gamma activity increase has been shown to be correlated with the local neuronal population spiking activity (Manning, Jacobs, Fried, & Kahana, 2009). The number of cycles (i.e., central frequency) of the wavelet was adapted as a function of frequency from 2 cycles at the lowest frequency to 10 cycles at the highest frequency. The wavelet transform was computed on each time-sample and the resulting amplitude envelope was downsampled by a factor of 4 (i.e., to a 128 Hz sampling rate). Amplitude was normalized across time and frequency to obtain the percentage of power change generated by the stimulus onset relative to the mean power in a pre-stimulus time-window (−700 msec to −300 msec relative to stimulus onset).

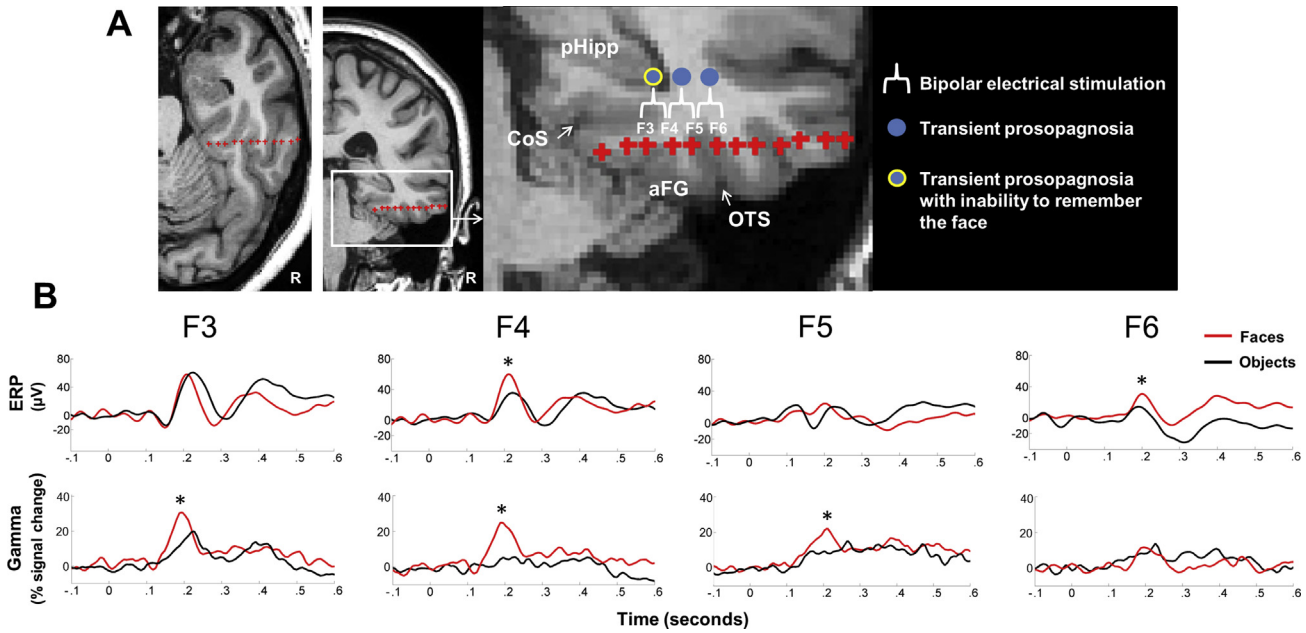

Fig. 2 – Anatomical and functional location of the stimulation sites inducing transient prosopagnosia: these sites were located in a face-selective region of the anterior FG. A. Anatomical location of electrode F (in red) and relevant contacts inducing transient prosopagnosia (F3, F4, F5, and F6). These contacts are located in the anterior FG (the posterior hippocampus, pHipp, is visible). B. Low- (ERP) and high-frequency (gamma: 30–160 Hz) electrophysiological responses to faces and objects recorded on these contacts. These contacts were face-selective in ERP and/or in gamma-ERSP. Abbreviations: aFG: anterior fusiform gyrus; OTS: occipito-temporal sulcus; CoS: collateral sulcus; pHipp: posterior hippocampus. *face-selective responses ($p < .01$).

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The amplitude difference between the gamma-band signal (30–160 Hz) generated by face and object stimuli was statistically assessed by running a permutation test at each time-sample of the response between −300 and 700 msec relative to stimulus onset. In short, the single-trial amplitudes obtained in the two conditions at a given time-point were randomly assigned in two bins, the number of trials in each bin being equal to the number of trials in each original condition. Next, the difference between the means of the two random bins was computed and stored. Because permutation shuffles the assignment of the conditions, the difference between the means of the two new bins reflects the difference between conditions under the null hypothesis. This process was performed 5000 times to generate a distribution of differences at a $p < .01$ (two-tailed) and values that reached this threshold for at least 10 consecutive milliseconds were considered as significant.

2.6. Face-selectivity: fMRI

The comprehensive methods (stimuli, stimulation procedures) used for this fMRI localizer study were the same as those used in several previous studies (summarized in Rossion et al., 2012).

2.6.1. Stimuli

Four categories of stimuli were used: photographs of faces (F), cars (C), and their phase-scrambled versions: scrambled faces (SF) and scrambled cars (SC). The face condition consisted of 43 pictures of faces (22 females) cropped so that no external features (hair, etc.) were revealed. All faces were shown in frontal view (for all stimulus information, see Rossion & Caharel, 2011). They were inserted in a gray rectangle. Similarly, the car condition consisted of 43 pictures of different cars in a full-front view also embedded in a gray rectangle. The scrambled stimuli were made using a Fourier phase randomization procedure (FFT with phase replaced by phase of a uniform noise) that yields images preserving the low-level properties of the original image (i.e., luminance, contrast, spectral energy, etc.), while completely degrading any category-related information. Pictures of faces/cars and the phase scrambled face/car pictures subtended equal shape, size and contrast against background.

2.6.2. Paradigm

The patient performed 3 runs of 11 min duration each. In each run, there were 6 blocks of 18 sec duration for each of the 4 types of stimuli. Blocks were separated by a baseline condition (cross fixation) of 9 sec. In each block, 24 stimuli of the same condition were presented (750 msec per stimuli, no ISI) on a black background screen, with 2 or 3 consecutive repetitions of the exact same stimulus in each block (target trials in the one-back task). This gave a total amount of 144 stimuli per category per run. The stimuli and the fixation cross were presented centrally, but stimulus location varied randomly in x (6%) and in y (8%) direction at each presentation. This change in stimulus location was made so that specific elements of the non-scrambled face and car stimuli (e.g., the eyes or headlights) do not appear at the same location at each trial, as it would be the case for scrambled stimuli even without jittering position. The patient performed a one-back identity task (2 or 3 targets per block).

2.6.3. Imaging acquisition parameters

Functional MR images of brain activity were collected using a 3T head scanner (Signa HDXT, GE Medical Systems, Milwaukee, WI) at the University Hospital of Nancy with repeated single-shot echo-planar imaging: echo time (TE) = 33 msec, flip angle (FA) = 77°, matrix size = 64 × 64, field of view (FOV) = 192 mm, slice thickness = 3 mm, repetition time (TR) = 2250 msec, 36 slices. A high-resolution anatomical volume of the whole brain was acquired using a T1-weighted sequence (resolution: 1 × 1 × 1 mm).

2.6.4. Data analysis

The fMRI signal in the different conditions was compared using Brain Voyager QX (Version 2.8.0, Brain Innovation, Maastricht, The Netherlands). Preprocessing consisted of a linear trend removal for excluding scanner-related signal, a temporal high-pass filtering applied to remove temporal frequencies lower than three cycles per run, and a correction for small interscan head movements by a rigid body algorithm rotating and translating each functional volume in 3D space. Functional data were smoothed in the spatial domain (FWHM 4 mm, all three directions), and spatially aligned with the high-resolution anatomical volume which was previously aligned to the AC-PC plane (automatic co-registration in Brain Voyager QX, adjusted manually). Subsequently, the functional data were analyzed using one multiple regression model [General Linear Model (GLM)] consisting of predictors, which corresponded to the particular experimental conditions of each experiment. The predictor time courses used were computed on the basis of a linear model of the relation between neural activity and hemodynamic response, assuming a rectangular neural response during phases of visual stimulation.

The contrast of interest was the conjunction contrast [(F-C) and (F-SF)]. This contrast was aimed at isolating the regions responding more to faces than non-faces objects, and for which this difference could not be accounted for by low-level visual cues (Rossion et al., 2012). The statistical threshold was set at $p < .01$ (uncorrected), corresponding to t-values above 2.58. A relatively liberal statistical threshold was used because the goal of the fMRI examination was not to test the whole brain but to assess whether the face-selective regions overlapped with the stimulated electrodes.

2.6.5. Intracerebral contact localization

The high-resolution T1 (aligned to the AC-PC plane) was fused with the post-operative CT-scan. The electrode contact coordinates were automatically extracted (MRI coordinates in the individual anatomy centered on the AC-PC plane). These electrode contact coordinates were then rendered in Brain Voyager software. The anatomical locations of relevant fMRI activations and intracerebral contacts were therefore assessed in the individual anatomy. Anatomical and functional volumes were also spatially normalized (Talairach & Tournoux, 1988) but only to determine Talairach coordinates of fMRI activations and intracerebral contacts.

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3. Results

3.1. Electrical stimulation of the anterior FG elicits transient prosopagnosia

Eight out of eight stimulations involving the right anterior FG and adjacent OTS induced a transient inability to recognize the face, i.e., transient prosopagnosia (stimulation of contacts F3–F4, F4–F5, F5–F6, Talairach coordinates: *x*: 29 to 45, *y*: −30, *z*: −18; see Fig. 2A for stimulation site location; see also Table 4). During the stimulation, the patient was unable to name or identify the famous faces presented (i.e., name or provide any semantic information about the person from his/her face). The patient stated: *"I didn't recognize him at first"*, *"I asked to myself, who is this person?"*, *"I'm not able to tell who this person is"* (see Videos S1, S2 and S3). Importantly, these stimulations never produced visual distortions of the face. When asked explicitly if the face was distorted, the patient responded: *"distorted? No, not at all"*, *"the face was not distorted"*. In most trials, the prosopagnosia stopped upon the termination of the stimulation (but see Video S2 for a persistent effect with 2 non-recognized faces just after the termination of the stimulation). In total, the patient did not recognize the 8 faces presented during stimulation of the right anterior FG (1 face per stimulation), and 2 faces presented immediately after 1 stimulation of contacts F3–F4 (performance during anterior FG stimulation: 0/8, 0%, see Table 4). In contrast, she immediately recognized and named the 41 remaining faces, either presented during stimulation of contacts outside the anterior FG (14 faces) or without stimulation (27 faces) (performance beside anterior FG stimulation: 41/43, 95.3%; see Table 4; performance during *vs* beside anterior FG stimulation: $p = .008$, Fisher's exact test). Stimulation of the right anterior FG did not evoke object recognition impairment (the 6 objects presented during the time of stimulation were correctly recognized, Table 3). Moreover, stimulations of contacts F3–F4 (right anterior FG) did not disrupt her face detection ability, since she was 100% correct at the face/object categorization task (23 stimuli in total, 17 during stimulation).

Supplementary video related to this article can be found at http://dx.doi.org/10.1016/j.cortex.2015.05.026.

When tested at the end of the stimulation procedure, CD was unable to remember specifically the non-recognized faces presented during the stimulation (3 stimulations of contacts F3–F4 in the right anterior FG, see Video S2 and S3). Across the 3 stimulations performed to test this point specifically, CD did not remember the 3 faces presented during stimulation (1 face per stimulation), but she correctly remembered 3 faces presented outside the stimulation and she correctly detected the 4 distractor faces. Therefore, in total, her accuracy rate at this task was 0% during stimulation (0/3) and 100% outside stimulation (7/7).

Stimulation of the right anterior FG never produced afterdischarges, epileptic spikes or epileptic seizures. Note also that the right anterior FG stimulation results were independent from the patient epilepsy: (i) contacts F3, F4, F5 and F6 never recorded epileptic spikes; (ii) the epileptic focus was found in the contralateral (left) hemisphere. Stimulation of contacts outside the right anterior FG did not produce any recognition impairment (contacts F1, F2, F7, F8, F9 of electrode F, contacts of electrode O; Tables 3 and 4).

3.2. Stimulation sites in the right anterior FG are located in a face-selective region

We tested the face-selectivity of each intracerebral contact by comparing electrophysiological responses to unknown faces and non-faces objects. Stimulated electrode contacts producing transient prosopagnosia (F3, F4, F5, F6) recorded larger responses to faces than non-face objects in ERP and/or in gamma-ERSP (ERP and gamma-ERSP: F4; ERP only: F6; gamma-ERSP only: F3 and F5, see Fig. 2B, see Engell & McCarthy, 2011 for a similar co-localization of these 3 types of responses in the human ventral temporal cortex). This shows that these contacts were located in a face-selective region of the anterior FG. On contacts F4 and F6, we recorded a positive face-selective ERP peaking at 200 msec after stimulus onset (Fig. 2B). On contacts F3, F4 and F5, we recorded significantly higher gamma band activity to faces compared to objects, starting from 100 msec and peaking at 200 msec after stimulus onset (Fig. 2B, see Supplementary Fig. S1 for time-frequency analyses). Contact F4, whose stimulation systematically evoked transient prosopagnosia (7 out of 7 stimulations) was the only face-selective contact both in ERPs and gamma-ERSP. Contacts of electrode F that were not associated with a face recognition impairment did not record face-selective responses (i.e., medial contacts F1 and F2 recorded larger responses for objects than for faces in both ERP and gamma-ERSP; lateral contacts F7, F8 and F9 did not record any visual responses). Contacts located in the right inferior occipital gyrus (O9, O10, O11) recorded face-selective ERPs but their stimulation did not produce face recognition impairment. However, this region was tested only once while presenting faces (1 stimulation on contacts O9–O10). In the left hemisphere, face-selective ERPs were observed in the FG (5 contacts: F′2, F′3, L′3, L′5, L′6) and in the inferior occipital gyrus (1 contact: O′8). These left face-selective contacts were not tested with faces during stimulation.

3.3. Stimulation sites are located anteriorly to the core face-processing network defined in fMRI

In fMRI, the conjunction contrast [(F-C) and (F-SF)] revealed typical face-selective activations of the core processing network (Figs. 3 and 4, Table 5). In the right hemisphere, we found the OFA in the inferior occipital gyrus, the pSTS the posterior section of the superior temporal sulcus and the FFA in the fusiform gyrus. Specifically, the right FFA was located in the posterior FG (posteriorly to the end of the hippocampus) in its lateral section (lateral FG, laterally to the mid-fusiform sulcus; Weiner & Grill-Spector, 2010; Weiner et al., 2014). We also found a face-selective activation in the left hemisphere (left FFA in the posterior FG). The left OFA was not found in fMRI but a face-selective ERP was found in the left inferior occipital gyrus. Taken together, all these left sided face-selective responses (left FFA in fMRI and intracranial face-selective ERPs in the left FG and left inferior occipital gyrus)

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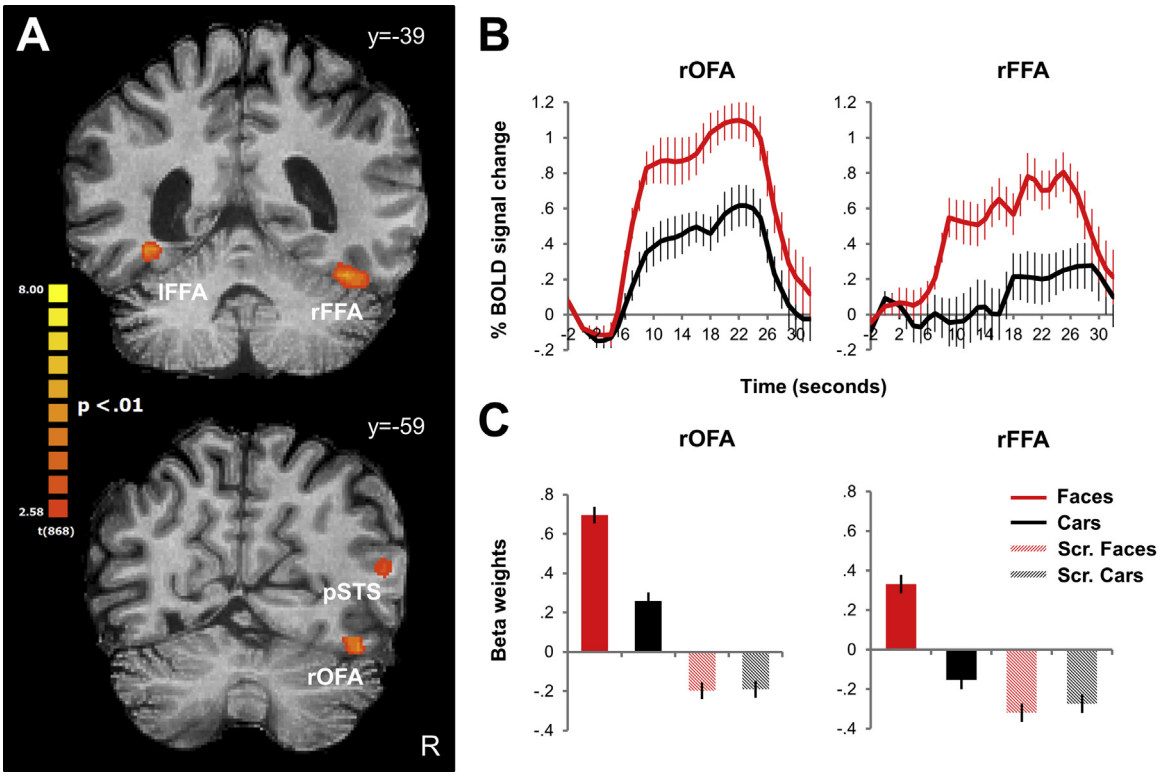

Fig. 3 – Patient CD shows a typical core face-processing network as revealed with fMRI. A. Face-selective areas of the core face-processing network on coronal slices [conjunction contrast (F-C) and (F-SF), $p < .01$ uncorrected]. B. BOLD time courses (right OFA and FFA). C. Beta weights (right OFA and FFA). Abbreviations: FFA: fusiform face area; OFA: occipital face area; pSTS: posterior superior temporal sulcus face-selective area. Vertical bars indicate standard errors.

suggest normal face processing functions in the left hemisphere, despite the patient's left temporal epilepsy.

Importantly, the electrode contacts whose stimulation led to transient prosopagnosia (F3, F4, F5 and F6) were located anteriorly to the right FFA (Fig. 4). More precisely, these contacts were located 8 mm forward of the anterior edge of the right FFA and 12 mm forward of the center of mass of the right FFA (*y* axis, native space). Although these contacts were located in a face-selective region, no face-selective activations overlapped the location of these contacts contrast [contrast (F-C) and (F-SF), $p < .01$ uncorrected, see Fig. 4]. No face-selective activations were found in 2-mm-diameter ROIs centered on

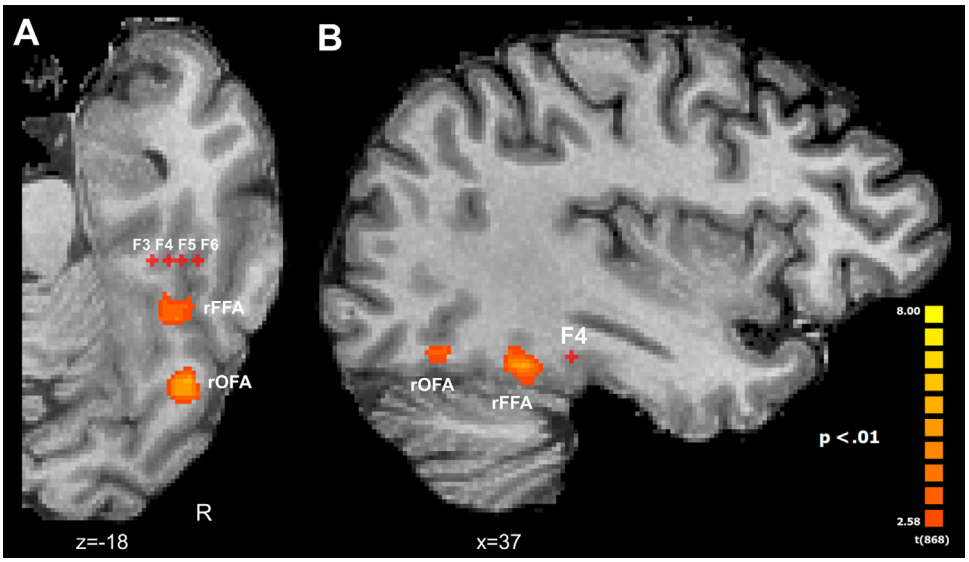

Fig. 4 – The critical stimulation sites eliciting transient prosopagnosia are located anteriorly to the core face processing network. A. Axial slice passing through electrode F contacts. B. Sagittal slice passing through contact F4.

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Table 5 – Talairach coordinates (center of mass), mean *t* and *p* values of face-selective activations of the core processing network identified in fMRI (conjunction contrast F-C and F-SF, $p < .01$ uncorrected).

	Talairach coordinates			Cluster size (number of voxels)	Mean *t* value	Mean *p* value
	x	*y*	*z*			
Right OFA	37	−60	−23	322	3.67	.0019
Right pSTS	52	−47	8	2001	3.26	.0027
Right FFA	37	−39	−26	589	3.42	.0022
Left FFA	−36	−37	−15	408	3.46	.0022

the location of each of the intracerebral contacts F3, F4, F5 and F6 ($p > .05$ for all ROIs using a contrast F-C). Moreover, no significant activation overlapped these contacts, even when using an unspecific contrast [(F + C)−(SF + SC), $p < .01$ uncorrected].

It is well known that a strong MRI signal drop-out occurs in the antero-inferior temporal cortex (Axelrod & Yovel, 2013; Ojemann et al., 1997). This signal drop-out is caused by susceptibility artifacts related to the local anatomy (mainly the ear canals). This may explain why we did not find any fMRI face-selective activation in the right anterior FG. When displaying fMRI face-selective activations and relevant contacts on raw functional slices (e.g., Rajimehr et al., 2009; Tsao et al., 2008), we observed indeed that the stimulation sites (contacts F3, F4, F5 and F6) lie within a severe signal drop-out involving the antero-inferior temporal cortex (Fig. 5A). For instance, the MRI intensity was around 3000 (scanner units) in the right FFA while it was around 300 in the vicinity of contact F4. This signal drop-out specifically involved the anterior FG and inferior temporal gyrus and spared more medial structures as the parahippocampal gyrus and adjacent collateral sulcus (Fig. 5B, see also Rajimehr et al., 2009).

4. Discussion

We report a case of transient inability to recognize faces following electrical stimulation of a face-selective region in the right anterior FG. This observation provides original evidence that a face-selective region of the right ventral temporal cortex anterior to the FFA is critical for face recognition.

4.1. *Electrically stimulating the anterior FG induces transient prosopagnosia*

As mentioned in the introduction, in Humans, previous evidence for a causal role of brain regions in face recognition come from lesion studies, TMS and intracerebral electrical stimulation. In right-handed individuals, this evidence systematically concerns the right hemisphere (see Bukowski, Dricot, Hanseeuw, & Rossion, 2013 and Rossion, 2014 for discussion of this issue of lateralization). Although studies of acquired prosopagnosic patients provide invaluable sources of information regarding the neuro-functional aspects of face recognition (Rossion, 2014), these patients usually have large and variable lesions, preventing to draw firm conclusions about the necessity of a specific region such as the anterior FG for face recognition (Barton, 2008; Barton, Press, Keenan, & O'Connor, 2002; Bouvier & Engel, 2006; Busigny et al., 2010; Sergent & Signoret, 1992; Sorger, Goebel, Schiltz, & Rossion, 2007). Moreover, these lesion studies cannot determine if the site of the lesion was face-selective prior to brain damage. TMS cannot be applied to ventral occipito-temporal areas (e.g., in the FG), so that TMS-evoked impairments in face processing have been found only following stimulation of the lateral occipital cortex (right OFA, e.g., Pitcher et al., 2007; Solomon-Harris et al., 2013) or of the lateral temporal cortex (pSTS, e.g., Dzhelyova, Ellison, & Atkinson, 2011). Moreover, these significant TMS effects concern decreases of a few percent in accuracy rates and/or increase in RTs in face discrimination tasks, but no interruption of the ability to recognize faces. Finally, in previous studies, electrical stimulation of the cortical surface of the posterior and middle FG caused visual distortion of real faces (Parvizi et al., 2012; Rangarajan et al., 2014). However, these latter studies do not report face recognition impairments. Thus, to our knowledge, prior to the present study, the only instance of an impairment of face recognition following electrical stimulation is the case of KV reported by Jonas et al. (2012). When stimulating the right OFA, KV was transiently unable to recognize famous faces along with face distortions for some stimulations.

Here, stimulating the right anterior FG induced transient prosopagnosia (i.e., inability to recognize faces) without any face distortions (i.e., the patient denied any such distortions when she was asked specifically, Video S1). Electrical stimulation of the anterior FG affected face recognition without affecting face/object categorization ability (i.e., face detection), as also sometimes observed following electrical stimulation of the FG (Chong et al., 2013). Moreover, here, the patient was subsequently unable to remember the presented faces that she did not recognize, suggesting that these faces were not encoded. This latest observation show that the impairment reported here was related to visual encoding/recognition rather than an impairment in face–name association as previously reported (e.g., Allison et al., 1994). Taken together, these observations indicate that we transiently evoked a prosopagnosia as typically described in chronically brain damaged patients: inability to recognize and encode faces, absence of conscious distortion of the face percept, and, in most cases, intact face detection ability (Barton, 2008; Busigny et al., 2010, 2014a; Rossion, 2014; Rossion et al., 2003a; Sergent & Signoret, 1992).

Without electrical stimulation, CD was able to discriminate/match pictures of unfamiliar faces and showed a typical face inversion effect. This shows that her face perception ability was in the normal range. Admittedly, a potential limitation of the present report is that CD's ability to recognize famous faces as evaluated by neuropsychological tests was below normal controls (CELEB test; Busigny et al., 2014b). This is not surprising since patients with temporal lobe epilepsy usually score below normal controls at famous face recognition and naming tests (Glosser et al., 2003). Unfortunately, face perception/recognition ability (i.e., discrimination of unfamiliar faces, familiar face recognition) was not tested in intracranial electrical stimulation studies that reported face perceptual distortions (Parvizi et al., 2012; Rangarajan et al., 2014; Vignal, Chauvel, & Halgren, 2000) or face–name association impairments (Allison et al., 1994). Therefore, we argue

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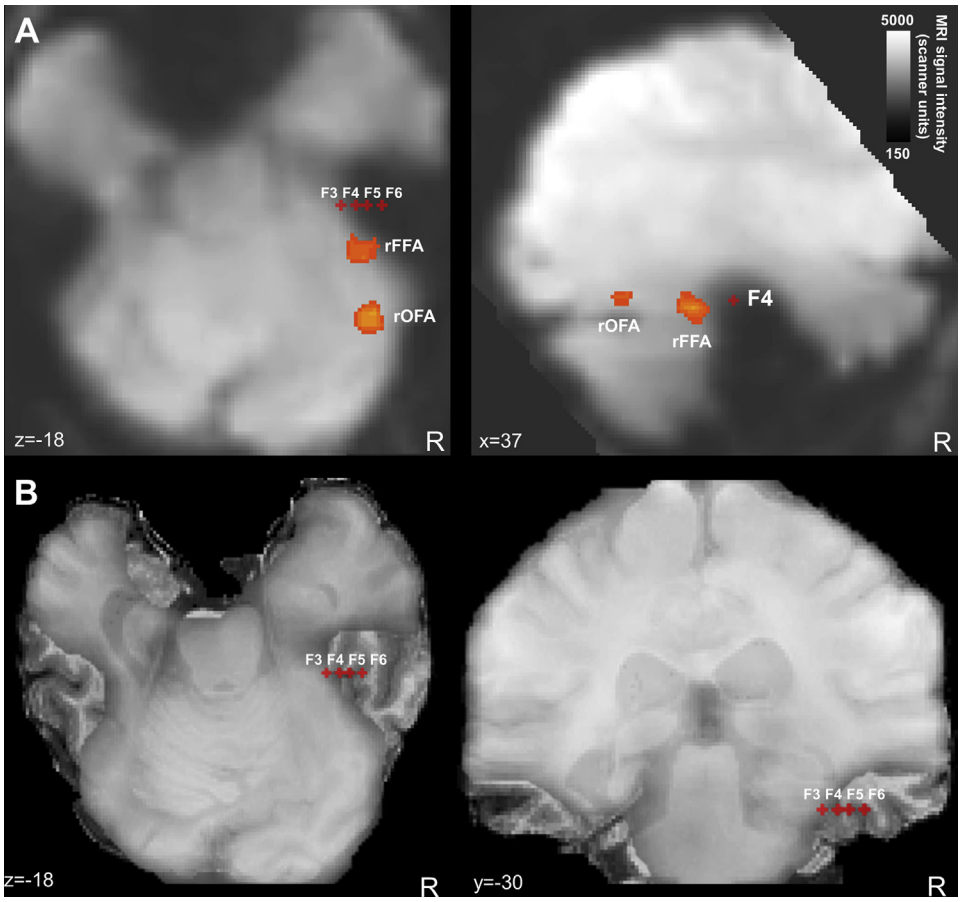

Fig. 5 – The critical stimulation sites are located in a MRI signal drop-out. A. Face-selective areas (rOFA and rFFA) and intracerebral contacts F3, F4, F5 and F6 are shown on raw functional slices (axial and sagittal slices). The MRI signal intensity shows a strong signal drop-out in the antero-inferior temporal cortex (in black), where these contacts are located. The right OFA and FFA are spared by this drop-out. B. Superimposition of raw functional and anatomical images (axial and coronal slices), showing that the signal drop-out specifically involved the anterior FG and the inferior temporal gyrus.

that the stringent neuropsychological evaluation performed here (as well as in Jonas et al., 2012) is a strength of the present study, and that such evaluations should be routinely performed in intracerebral stimulation studies. In this context, there are at least two arguments suggesting that CD's difficulties with face recognition outside of the stimulation cannot account for the transient prosopagnosia observed during intracerebral stimulation. First, the neuropsychological test assessing famous face recognition performance (CELEB) was quite difficult, using faces without external features and limited presentation times. In contrast, the faces shown during the stimulation had external features, and were presented until response. Second, beside anterior FG stimulation, CD's performance at recognizing famous faces with such pictures was almost perfect (41 out of 43 famous faces, 95.3%), while she was completely unable to recognize any of the famous faces during anterior FG stimulation (0/8, 0%).

4.2. *Specificity and nature of the functional impairment*

Even though we did not test famous non-face objects (such as famous places, Jonas et al., 2012), several considerations suggest that CD's recognition impairment was specific to faces. Firstly, the anatomical location of the stimulation sites was relatively distant from medial temporal structures (hippocampus, rhinal cortex), involved in recognition memory and long-term memory representations. Secondly, the patient was not impaired at recognizing common non-face objects when stimulating the anterior FG. Thirdly, the stimulation sites were located in a face-selective cortical region, as shown by the intracerebral face-selective responses in ERP and in the gamma band recorded within this region. Moreover, as responses recorded in the gamma band typically reflect local cortical activity (Crone, Miglioretti, Gordon, & Lesser, 1998; Manning et al., 2009; Miller et al., 2007), this shows that face-selective responses were generated by a local face-selective region of the right anterior fusiform gyrus.

Given the reported absence of face distortion, it may be tempting to interpret CD's deficit as a form of "associative prosopagnosia", namely an impairment of face recognition despite an intact percept (Davies-Thompson, Pancaroglu, & Barton, 2014; De Renzi, 1986; Gainotti & Marra, 2011; McNeil & Warrington, 1991; Sergent & Signoret, 1992), and to contrast it with the kind of "apperceptive prosopagnosia"

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evoked by stimulating the OFA (Jonas et al., 2012, 2014) and FFA (Parvizi et al., 2012; Rangarajan et al., 2014). However, the distinction between perception and memory impairments in neuropsychological patients with (prosop)agnosia (or in congenital/developmental forms of prosopagnosia) is not clear-cut (Farah, 1990; Rossion, 2014). That is, so-called pure associative cases of prosopagnosia usually perform below normal range at matching different pictures of unfamiliar faces or use extremely slow and painstaking strategies (e.g., Davidoff & Landis, 1990; Delvenne, Seron, Coyette, & Rossion, 2004; Farah, 1990; Levine & Calvanio, 1989), even when brain damage is restricted to anterior regions (e.g., Busigny et al., 2014a). Hence, given that CD was not tested with simultaneous matching of unfamiliar face pictures, there is no objective evidence that her percept was intact, and thus one should remain cautious in interpreting CD's transient impairment as reflecting a form of associative prosopagnosia.

4.3. *The anterior FG: an undefined face-selective region*

The critical stimulation site in the anterior FG was located anteriorly to the right FFA individually identified in CD's brain. This right FFA was localized in the posterior and middle FG (Talairach *y* axis: −39), a localization fully consistent with the typical localization of the right FFA (Talairach *y* axis around −40/−70; e.g., Fox, Iaria, & Barton, 2009; Kanwisher et al., 1997; Rossion et al., 2012). Moreover, the stimulation site was located anteriorly to the most anterior FFA cluster when the FFA is separated into 2 clusters along the FG, as in some recent studies (e.g., "mFus-faces/FFA-2", Weiner & Grill-Spector, 2010; Weiner et al., 2014). Indeed, this most anterior FFA cluster is located in the middle FG at the level of the mid-fusiform sulcus (Weiner et al., 2014), whereas our stimulation site was located in the anterior FG, where the mid-fusiform sulcus is not visible (Fig. 3A). However, it is important to note that the critical stimulation site was located posteriorly to most anterior fMRI face-selective activations found in the ventral temporal lobe, these activations being generally found in the anterior segment of the collateral sulcus (Talairach *y* axis around 0/−10; Avidan et al., 2014; Axelrod & Yovel, 2013; Nasr & Tootell, 2012; Pinsk et al., 2009; Pyles, Verstynen, Schneider, & Tarr, 2013; Rajimehr et al., 2009; Rossion et al., 2012; Tsao et al., 2008).

In sum, our critical stimulation site was located anteriorly to the FFA but posteriorly to the most anterior face-selective activations in the ventral temporal lobe. In fMRI, these "intermediate" ventral temporal face-selective activations have been reported specifically in the anterior FG in a handful of studies (Talairach *y* axis around −30; Axelrod & Yovel, 2013; Nasr & Tootell, 2012; Pyles et al., 2013; Rossion et al., 2012). However, anterior FG face-selective activations were rarely reported and were not consistently found in individual subjects in these studies due to a hemodynamic signal drop-out created by magnetic susceptibility artifacts (Axelrod & Yovel, 2013; Ojemann et al., 1997; Rajimehr et al., 2009; Tsao et al., 2008). Consistently with these observations, we were unable to find fMRI face-selective activations overlapping the relevant stimulation sites due to a severe signal drop-out affecting specifically the anterior FG, even though we recorded local ERP and gamma face-selective responses showing the face-selectivity of this region. This hemodynamic signal drop-out in fMRI may also explain why little is known about the role of anterior FG face-selective region in face processing (beyond PET studies, see below). In this context, our study illustrates the value of both intracerebral recordings, revealing highly significant local ERPs and gamma band face-selective responses here in the anterior FG, and electrical stimulation for better understanding face-selective regions anterior to the FFA and thus the function of the whole cortical face network.

Although intracerebral electrical stimulations are focal (thanks to low intensity stimulations of small contacts directly embedded into the gray matter), the stimulation signal may propagate to other connected face-selective areas throughout white matter tracts (Gomez et al., 2015; Gschwind, Pourtois, Schwartz, Van De Ville, & Vuilleumier, 2012; Pyles, et al., 2013).[1] In monkeys, microstimulation of face-selective patches has been shown to produce activation in other face patches (Moeller, Freiwald, & Tsao, 2008). However, the specific connectivity of the face-selective anterior FG region remains unknown so that the propagation of the stimulation signal is difficult to estimate (Gschwind et al., 2012; Pyles, et al., 2013). One potential reason for this lack of knowledge is that fMRI-tractography studies have so far failed to localize this face-selective region in a sufficient number of participants. For instance, one study identified face-selective activations in the anterior FG in 2 subjects only, so that the specific connectivity of this region was not examined further (Pyles, et al., 2013).

4.4. *What is the role of the right anterior FG in face processing?*

Using famous faces, we showed that the right anterior FG is critical for familiar face recognition. This suggests that the anterior FG plays a role in person identification and memory. This hypothesis is consistent with fMRI and brain lesions studies showing that anterior temporal lobe may play a role in face individualization and semantic knowledge about people (e.g., Busigny et al., 2014a; Joubert et al., 2006; Kriegeskorte, Formisano, Sorger, & Goebel, 2007; Nestor, Plaut, & Behrmann, 2011; Sergent et al., 1992; Von Der Heide, Skipper, & Olson, 2013; for reviews see Collins & Olson, 2014; Gainotti, 2007; Gobbini & Haxby, 2007; Olson, Plotzker, & Ezzyat, 2007). However, these studies rarely investigated the role of the anterior FG specifically. As discussed above, fMRI studies rarely reported activation in this region since fMRI signal is notoriously weak in the anterior FG. Brain lesions studies have concentrated on anterior temporal lobe damaged patients following stroke, trauma, neurodegenerative disorder (such as fronto-temporal dementia) or cortical resection. These lesions were usually large or undefined, extending from

[1] It is very unlikely that our stimulation effects were solely related to the stimulation of white matter tracts connected with more posterior face-selective areas, for several reasons: (i) the stimulated contacts were located in the gray matter; (ii) stimulation of adjacent contacts in the white matter did not evoke any recognition impairment (e.g., contact F7); (iii) the stimulation sites were located in a face-selective cortical area; (iv) only contacts showing face-selective responses were associated with face recognition impairment.

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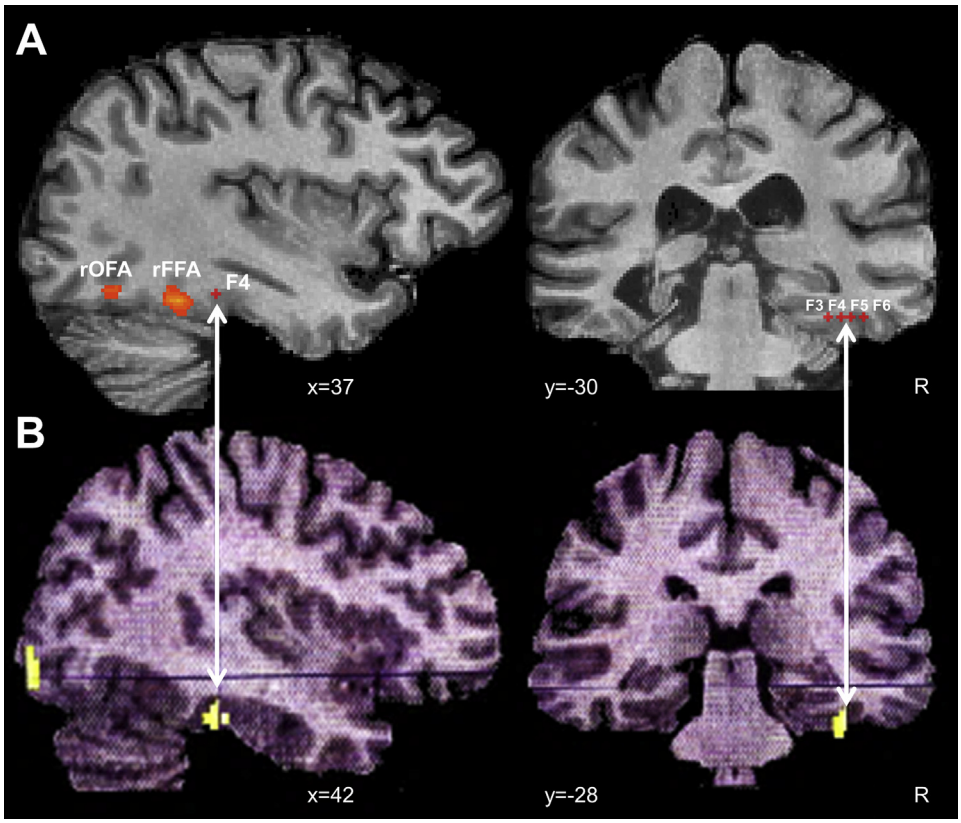

Fig. 6 – The critical stimulation sites overlap the location of PET activations for familiar faces (Rossion et al., 2001). Comparison of the locations of the stimulated region in the present study (A.) and the differential activation for familiar and unfamiliar faces in the PET study of Rossion et al. (2001) (B.), in sagittal and coronal slices. The right anterior FG PET activation displayed below (Talairach coordinates: x: 42, y: −28, z: −24) was anterior to the localized right FFA (x: 38, y: −44, z: −28; Rossion et al., 2003b).

the middle ventral temporal cortex to the temporal pole, and thus not specific to the anterior FG.

Overall, our findings regarding the critical function of the right anterior FG relate better to two independent, and rather unusual, observations. First, two early studies using PET, in which there is no issue of signal drop-out to consider in these regions, identified the right anterior FG in a contrast between familiar and unfamiliar faces (Rossion, Schiltz, Robaye, Pirenne, & Crommelinck, 2001; Wiser et al., 2000). In the first of these studies, the right anterior FG signaled a clear-cut (i.e., categorical) difference between familiar and unfamiliar faces in an orthogonal task (Rossion et al., 2001). The localization of the focus of activation strikingly corresponds to the site of stimulation evoking prosopagnosia here (Fig. 6), and was clearly distinct from the right FFA as defined independently in the same group of subjects (Rossion, Schiltz, & Crommelinck, 2003b). Second, a study investigating the anatomical structure of the fusiform gyrus in congenital prosopagnosic patients reported specifically a volume reduction of the anterior FG in these patients compared to normal controls (Behrmann, et al., 2007). Moreover, this volumetric reduction of the anterior FG was correlated with participants' behavioral decrement in famous face recognition. Taken together, these studies and the present original report point to the right anterior FG as a critical node for distinguishing familiar and unfamiliar faces and thus recognizing familiar faces.

5. Conclusion

To our knowledge, this is the first report of transient impairment of familiar face recognition with no evidence of perceptual face distortion, and following electrical stimulation a face-selective region anterior to the middle fusiform gyrus. These findings point to the causal role in face recognition of the right anterior fusiform gyrus and more generally of face-selective regions located beyond the OFA and FFA, i.e., anteriorly to the so-called "core" cortical network for face processing in humans.

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Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.cortex.2015.05.026.

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