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Intracerebral electrical stimulation to understand the neural basis of human face identity recognition

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Abstract

Recognizing people's identity by their faces is a key function in the human species, supported by regions of the ventral occipito-temporal cortex (VOTC). In the last decade, there have been several reports of perceptual face distortion during direct electrical stimulation (DES) with subdural electrodes positioned over a well-known face-selective VOTC region of the right lateral middle fusiform gyrus (LatMidFG; i.e., the "Fusiform Face Area", FFA). However, transient impairments of face identity recognition (FIR) have been extremely rare and only behaviorally quantified during DES with intracerebral (i.e., depth) electrodes in stereo-electroencephalography (SEEG). The three detailed cases reported so far, summarized here, were specifically impaired at FIR during DES inside different anatomical VOTC regions of the right hemisphere: the inferior occipital gyrus (IOG) and the LatMidFG, as well as a region that lies at the heart of a large magnetic susceptibility artifact in functional magnetic resonance imaging (fMRI): the anterior fusiform gyrus (AntFG). In the first two regions, the eloquent electrode contacts were systematically associated with the highest face-selective and (unfamiliar) face individuation responses as measured with intracerebral electrophysiology. Stimulation in the right AntFG did not lead to perceptual changes but also caused an inability to remember having been presented face pictures, as if the episode was never recorded in memory. These observations support the view of an extensive network of face-selective VOTC regions subtending human FIR, with at least three critical nodes in the right hemisphere associated with differential intrinsic and extrinsic patterns of reentrant connectivity.

KEYWORDS

direct electrical stimulation, face identity, human face recognition, prosopagnosia, SEEG

1 | INTRODUCTION

A fundamental function of central nervous systems is to recognize stimuli in their physical and social environment. In humans, recognition of the identity of people based on their faces (Face Identity Recognition, FIR) arguably constitutes the most challenging, socially ecological, recognition function. FIR is extremely difficult, for three main reasons. First, while individual faces most likely differ more in humans than in other animal species (Sheehan & Nachman, 2014), all human faces, in particular within a genetically homogenous group, share similar features

and their overall configuration. Thus, FIR requires fine-grained visual discrimination processes. Second, the same face identity can vary substantially under different viewing conditions, to the point where two views of the same face identity often differ physically to a larger extent than two different facial identities (Burton et al., 2016). Therefore, FIR requires high-level generalization of a specific response across different facial views. Third, given the large number of faces encountered and the fact that the number of individuals encountered change over time in most modern human societies, the number of facial identities to recognize is extremely large and undetermined. Despite this challenge, in humans, identity recognition is primarily based on the face, which, among all body parts, carries by far the largest source of morphological and genetic diversity in a homogenous population (Sheehan & Nachman, 2014). Human adults are able to recognize the identity of thousands of faces on average (Jenkins et al., 2018), rapidly (i.e., at a glance, and within a few hundreds of milliseconds of processing; Hsiao & Cottrell, 2008; Jacques et al., 2007; Visconti di Oleggio Castello & Gobbini, 2015) and largely automatically (i.e., not under volitional control) (Zimmermann et al., 2019).

Understanding the neural basis of human FIR has, for long, relied on observations of patients with *prosopagnosia*—a sudden, massive and selective impairment of FIR following brain damage (Bodamer, 1947; for a recent review of the functional aspects of prosopagnosia, see Rossion, 2018a). Lesions of these patients most consistently concern regions of the ventral occipito-temporal cortex (VOTC), with a right hemispheric dominance (Barton, 2008; Bouvier & Engel, 2006; Cohen et al., 2019; Hécaen & Angelergues, 1962; Meadows, 1974; Sergent & Signoret, 1992). To clarify the neural basis of FIR, functional neuroimaging studies have contrasted the presentation of familiar and unfamiliar faces, or of different unfamiliar face identities, searching for differences either in terms of overall magnitude of hemodynamic response (i.e., univariate analysis) or in terms of changes in the pattern of activity across voxels (i.e., multivariate pattern analysis; MVPA). Overall, while some studies have disclosed differences between (patterns of) neural activity evoked by different individual faces in several VOTC regions, it is fair to say that these effects obtained with MVPA are rather small, unreliable, and inconsistent across experiments (Anzellotti et al., 2014; Goesaert & Op de Beeck, 2013; Kriegeskorte et al., 2007; Natu & O'Toole, 2011; Nestor et al., 2011) probably because each voxel contains millions of neurons (Logothetis, 2008) involved in coding numerous facial identities (see the critical views of Kanwisher, 2017; Rossion, 2014; Dubois et al., 2015). Studies measuring repetition suppression effects for (usually unfamiliar) pictures of facial identities have more consistently reported significant effects in predefined regions of the VOTC responding selectively to faces such as the "Occipital Face Area" (OFA, in the inferior occipital gyrus, IOG) and the "Fusiform Face Area" (FFA, in the lateral middle fusiform gyrus, LatMidFG) (e.g., Gauthier et al., 2000; Gilaie-Dotan et al., 2010a; Ewbank et al., 2013; Hermann et al., 2017; Kovács, 2020 for review) but without systematically exploring other brain regions.

Besides these limitations, neuroimaging studies cannot directly inform about the *critical* function(s) of VOTC regions in FIR (Sergent et al., 1992). Real cases of prosopagnosia[1] following brain damage remain very rare, and their brain lesions are often quite large and variable across patients (e.g., Barton et al., 2008; Cohen et al., 2019; Sergent & Signoret, 1992) making it difficult to precisely identify critical brain regions, or nodes of a cortical network, subtending FIR. Given their ventral and relatively medial location, key VOTC regions for FIR are not accessible to transcranial magnetic stimulation (TMS), except for the lateral section of the IOG. While TMS stimulation over the right IOG/OFA can disrupt FIR (Pitcher et al., 2007), this effect is not always consistent across studies (e.g., Ambrus et al., 2017; Bona et al., 2018); Gilaie-Dotan et al., 2010b; Pitcher et al., 2008; Solomon-Harris et al., 2013), perhaps due to the distance between the stimulation site and the targeted neural population and/or to remote and diffuse effects to downstream cortical areas (Groen et al., 2021; Solomon-Harris et al., 2016).

In this context, direct brain stimulation (DES) in patients with tumours or epilepsy is a powerful technique for inferring the critical function of brain regions in humans and could be highly informative about the neural basis of FIR. Through the application of electrical current with a bipolar electrode to the cortex, DES allows to temporarily disrupt the function(s) of the stimulated region in order to simulate what would be the behavioral effect if this region was removed or lesioned (Borchers et al., 2011; Desmurget et al., 2013; Ojemann et al., 1989; Penfield, 1958). DES in epileptic subjects is not performed intraoperatively, but through electrodes implanted intracranially for several days or weeks to define the localization and extent of epileptic seizures, allowing more carefully controlled stimulation procedures even in a clinical context.

In practice, they are two possible surgical techniques for intracranial electrodes placement (Figure 1). On the one hand, electro-corticography (ECOG, Wyler et al., 1984) consists in applying electrodes onto the cortical surface after removing part of the skull (i.e., subdural electrodes). Subdural electrodes have a circular shape and are spatially

[1]The definition of prosopagnosia used here excludes developmental disorders at FIR in the absence of neurological history, often referred to as *developmental*, or *congenital, prosopagnosia* (Behrmann & Avidan, 2005; Duchaine & Nakayama, 2006) but more accurately as *prosopdysgnosia* (Rossion, 2018b; Sorensen & Overgaard, 2018).

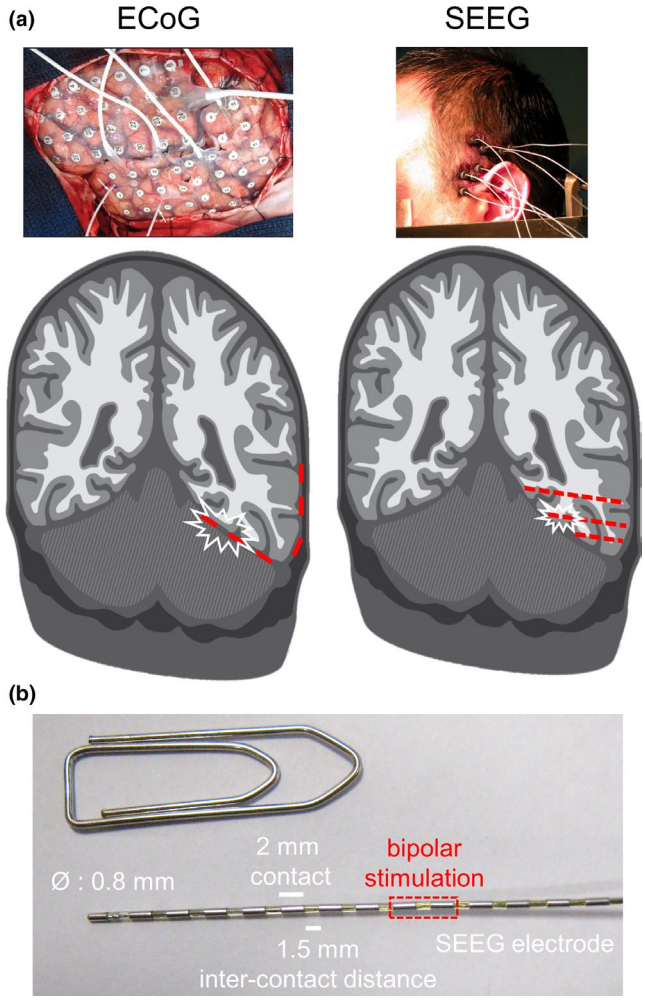

FIGURE 1 ECOG and SEEG methods. (a) Two types of intracranial electroencephalography techniques for recording and stimulation: ECOG and SEEG. Above, pictures of the surgical procedure involved in placing the intracranial electrodes. In ECOG, part of the skull is removed to apply electrodes onto the cortical surface (here, grids of electrodes). In SEEG, small holes are drilled into the skull to implant thin depth or intracerebral electrodes. Below, schematic coronal representation of intracranial electrodes in contact with the middle fusiform gyrus. The electrodes are represented in red. Bipolar stimulations (schematically represented in white) are in both cases applied between 2 adjacent recording sites. (b) Photograph of a typical SEEG electrode (showed close to a paper clip for size comparison), consisting of a cylinder of 0.8 mm diameter containing 8–15 independent recording contacts of 2 mm in length separated by 1.5 mm from edge to edge and by 3.5 mm center-to-center. The dotted rectangular area displays the electrode length involved in a bipolar stimulation

arranged as grids or strips with typically 5 to 10 mm inter-electrode spacing (center-to-center). On the other hand, stereo-electroencephalography (SEEG, Talairach & Bancaud, 1973) consists in inserting electrodes inside the brain, from the cortical surface to the medial cortex or medial temporal lobe structures (i.e., intra*cerebral* electrodes, also often referred to as *depth* electrodes). The current intracerebral electrodes are thin cylinders (e.g., 0.8 mm diameter) typically containing 8–15 contiguous individual recordings sites (or contacts) separated by an insulating material (3.5 mm spacing, center-to-center) (Figure 1b). From the point of view of fundamental research, each technique has its own advantages: while ECOG offers a more extensive spatial coverage, more homogenous across individual brains, SEEG provides recordings directly inside the grey matter, allowing the specific exploration of cortical sulci and medial temporal lobe structures (e.g., amygdala, hippocampus). These respective advantages of ECOG and SEEG apply to electrophysiological recordings (Rossion et al., 2018; George et al., 2020), but also to DES: while the wider coverage of ECOG electrodes allows more common sites to be stimulated across individuals and may even promote (small) group studies (e.g., Sanada et al., 2021; Schrouff et al., 2020), the electrodes are not inserted inside the cerebral matter, preventing to stimulate cortical sulci and medial temporal lobe structures, but also requiring higher current intensity to elicit potentially less specific behavioural effects than with depth electrodes (SEEG).

In the early ECOG studies focusing on intracranial potentials in response to face stimuli (e.g., N200), facial hallucinations and transient disruption of famous face naming were noted in several individuals following DES to various VOTC sites (Allison et al., 1994; Puce et al., 1999). More recently, ECOG studies focusing on DES (of the LatMidFG) have reported face-related perceptual changes (i.e., changes in the phenomenological experience of the face stimulus, usually a distortion of the experimenter's face in front of the subject or a presented picture; Parvizi et al., 2012; Rangaranjan et al., 2014; Schalk et al., 2017; Schrouff et al., 2020; Sanada et al., 2021; see also Mundel et al., 2003). However, there was no FIR impairment during DES at a face naming task in the case study reported by Parvizi and colleagues (2012) and, to our knowledge, none of the other recent studies evaluated FIR. More generally, behavioral FIR during DES with ECOG has not been thoroughly studied, objectively quantified and related to neural measures of face-selectivity and FIR. This contrasts with the few SEEG DES studies of FIR performed over the last decade, which are therefore described in more detail and form the basis of the present review.

2 | THREE CASES OF TRANSIENT IMPAIRMENT IN FIR DURING DES

2.1 | KV: A (first) case of transient prosopagnosia following right IOG stimulation

A first case of transient impairment of FIR during SEEG DES (i.e., "transient prosopagnosia") was reported by Jonas and colleagues in 2012. During stimulation of a region of the

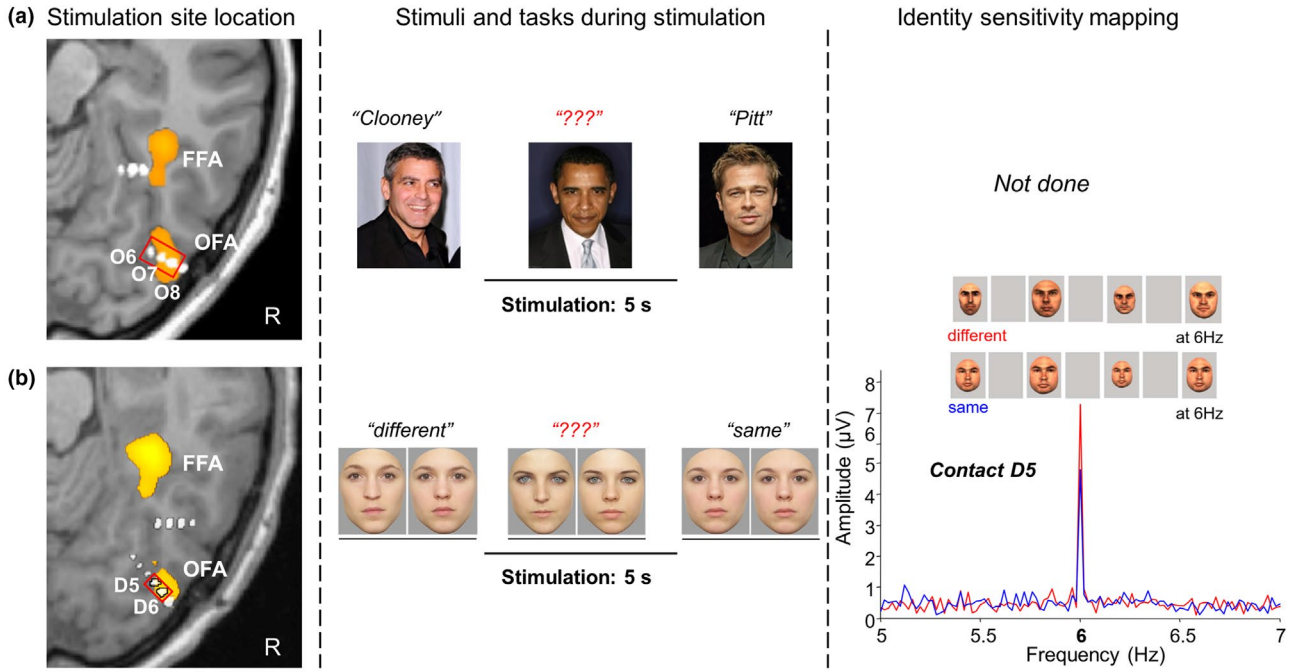

FIGURE 2 Stimulating the right IOG induces transient FIR impairment (subject KV, case 1). (a) From Jonas et al., (2012). (b) Jonas et al., (2014). In both studies, the left panel shows the fMRI face-selective activations in the right VOTC (axial slices) with the SEEG electrodes superimposed (white dots); the middle panel shows the stimuli presented during the stimulation procedure; the right panel shows SEEG recordings during a FPVS paradigm measuring sensitivity to face identity. In Jonas et al., (2012), the eloquent contacts O6, O7 and O8 are located in the right face-selective IOG ("OFA") as shown by fMRI (shown here) and face-selective ERPs recorded on these contacts. Stimulation of these contacts induced a transient inability to recognize famous faces. In Jonas et al., (2014), stimulating two contacts located within the right face-selective IOG (D5 and D6) evoked a transient inability to discriminate unfamiliar face identities. During SEEG, KV was shown with a FPVS adaptation paradigm measuring sensitivity to face identity at a fast rate of 6Hz, with either identical faces or different faces (Rossion & Boremanse, 2011). The significantly largest difference for different versus same faces was found on the eloquent contact D5 (right panel shows responses to different and same upright faces at 6Hz in the frequency domain)

	# of FIR impairment	# of perceptual changes	# of non-face objects impairment
Case 1, KV (Jonas et al., 2012): right IOG	6/7	4/6	0/4
Case 1, KV (Jonas et al., 2014): right IOG	6/6	6/6	0/1
Case 2, MB (Jonas et al., 2018): right LatMidFG	6/6	6/6	0/2*
Case 3, CD (Jonas et al., 2015): right AntFG	8/8	0/8	0/3

Note: The perceptual changes refer either to a disturbance in perceiving the spatial relationship of facial elements (KV, Jonas et al., 2012), to a visual change making 2 different faces looking the same (KV, Jonas et al., 2014), or to an hallucination of individual face parts appropriately integrated within the perceived face (MB, Jonas et al., 2018). For a complete report of the number of stimulations across all electrode contacts or trials without stimulation, see the papers referred in the table. *Although subject MB (case) was not impaired with non-face objects, she reported face hallucinations for two presentations of non-face stimuli (see text).

TABLE 1 For each eloquent site evoking reproducibly FIR impairments when stimulated, number of stimulations evoking FIR impairments, face perceptual changes and impairments for non-face objects (objects or famous scenes)

right IOG (stimulation of two pairs of contacts, Figure 2a), subject KV was suddenly unable to recognize photographs of famous faces (Video 1). This effect was highly reproducible (Table 1) and transient, that is, ending as soon as the stimulation stopped. Across various trials, while being naïve to the purpose of the experiment (and of course not feeling any direct effect of brain stimulation), KV reported a subjective experience of not being able to perceive the face as a

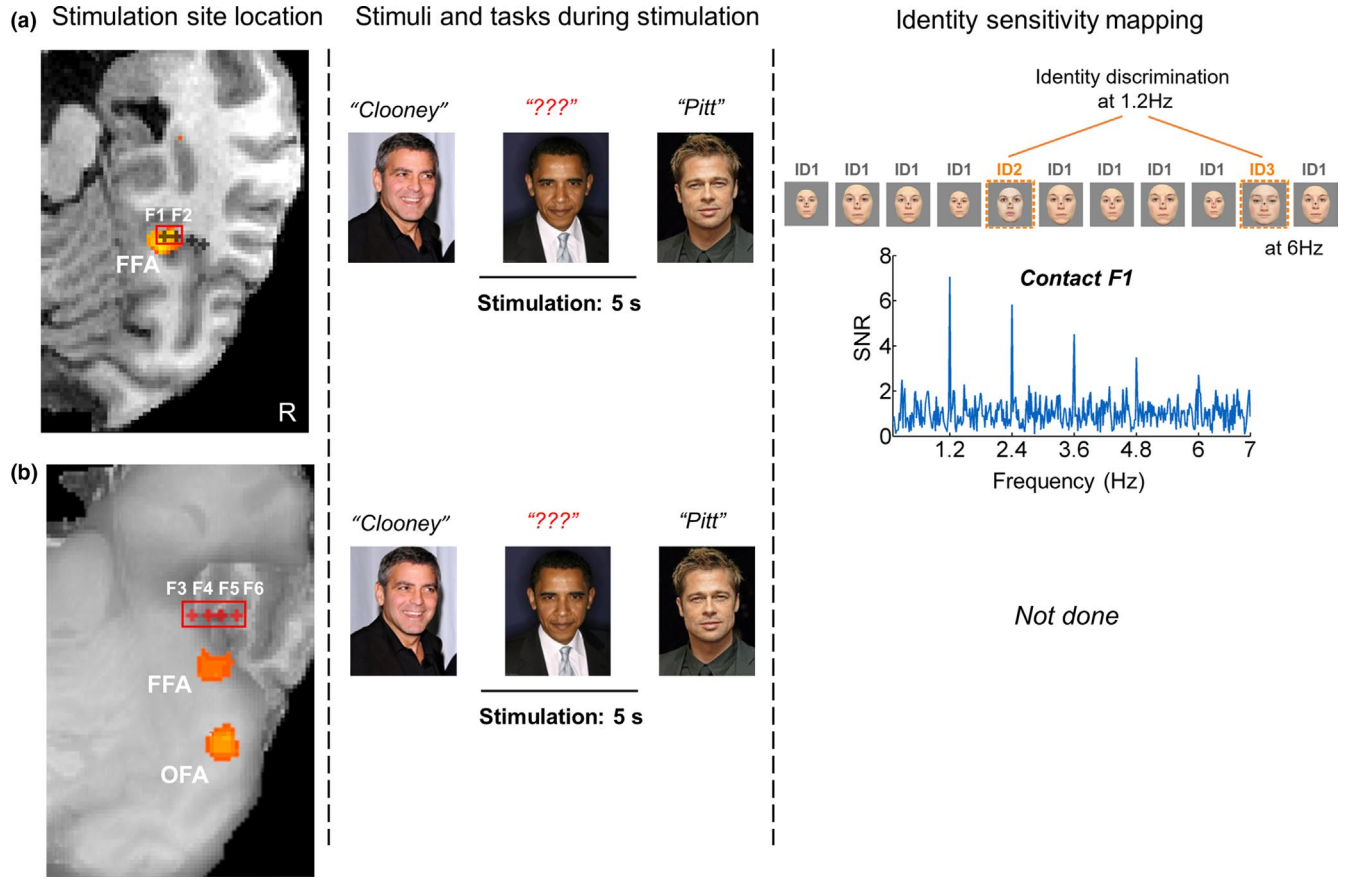

FIGURE 3 Stimulating the LatMidFG and AntFG induces transient FIR impairment (above: subject MB, case 2; below: subject CD, case 3). (a) Study of Jonas et al., (2018) in the right LatMidFG (subject MB). (b) Study of Jonas et al., (2015) in the right AntFG (subject CD). In both studies, the left panel shows fMRI face-selective activations in the right VOTC (axial slices) with SEEG electrodes superimposed (black or red crosses); the middle panel shows the stimuli presented during DES; the right panel shows SEEG recordings during a FPVS paradigm measuring sensitivity to face identity (Liu-Shuang et al., 2014; Rossion et al., 2020). In subject MB, the eloquent contacts (F1 and F2) were located in the face-selective LatMidFG ("FFA") as shown by fMRI and intracerebral face-selective responses. During SEEG, subject MB was shown with a FPVS "oddball" paradigm measuring sensitivity to face identity containing sequences with an unfamiliar face identity presented at a fast rate of 6 Hz, with different unfamiliar face identities inserted every 5th image (identity change frequency = 1.2 Hz, that is, 6 Hz/5). On contact F1, large face identity discrimination responses were recorded (right panel shows identity discrimination responses at 1.2 Hz and harmonics in the frequency domain, in a signal-to-noise ratio (SNR) spectrum). Of all the 137 recorded contacts in MB's brain, contact F1 recorded, by far, the largest face identity discrimination response amplitude. In subject CD, the eloquent contacts (F3 to F6, inducing a transient inability to recognize famous faces) were located in the right AntFG, anteriorly to the FFA. Despite large face-selective responses in SEEG on these contacts, fMRI face-selective activations were not found because of a severe signal drop-out affecting the right AntFG (the left panel displays the raw functional images in light grey, showing the eloquent contacts being located in a region with very low fMRI signal)

whole ("the face does not appear to me as a single entity"), or a visual change with the facial elements in disarray ("the facial elements were mixed") (Video 1). However, in some trials in which KV failed to recognize the face identity, there was no change of percept at all (Video 1).

2.2 | MB (case 2): Intracerebral stimulation of the right lateral fusiform gyrus produces face identity palinopsia

Given the high and consistent face-selective responses found in the right LatMidFG, that is, the FFA, it is not surprising that this region has been the focus of most ECOG DES studies investigating the processing of faces (Mundel et al., 2003; Parvizi et al., 2012; Rangaranjan et al., 2014; Sanada et al., 2021; Schalk et al., 2017; Schrouff et al., 2020). While SEEG studies performed in large populations of subjects have also identified the largest face-selective neural responses in this region (Hagen et al., 2020; Jonas et al., 2016), only one case of intracerebral stimulation has been reported so far: subject MB who, during stimulation inside the right LatMidFG (Figure 3a, Table 1) experienced facial *palinopsia*, that is, hallucinations of facial elements appropriately incorporated in the face identity in front of her (Video 2) (Jonas et al., 2018). MB experienced this phenomenon for the faces

of a clinician or experimenter in the room in front of her ("I saw you with eyes and ears which were not yours") (Video 2). Although she stated that the superimposed features were those of a familiar face, she was unable to determine the identity of that face. She was also tested more systematically with photographs, stating, for example, that "the photograph of Nicolas Sarkozy [former French president, first presented face picture during stimulation] *was transposed onto the other face identity* [second presented face picture during stimulation]". MB never reported aberrant facial configurations, and reproducibly stated that the facial structure was preserved ("it was a normal face").

2.3 | CD (case 3): Transient prosopagnosia beyond the posterior cortical face network

The third case of transient selective impairment to recognize famous faces' identities during SEEG DES followed intracerebral stimulation inside a region located anteriorly to the right LatMidFG, that is, in the anterior fusiform gyrus (AntFG; Figure 3b) located in the anterior temporal lobe (ATL). When stimulated in this region, subject CD was transiently unable to recognize any famous face picture presented (Jonas et al., 2015; Video 3, Table 1). As for subject KV, this behavioral impairment was clear, massive, and highly reproducible. After stimulation, CD was asked why she did not name or expressed any sign of recognition of the famous face identity shown during stimulation: "I didn't recognize the face", "I asked to myself, who is this person? … I'm not able to tell who this person is", "Am I stupid or what?". When specifically asked if the face was distorted, CD expressed her surprise: "Not at all", "The face was not distorted" Shortly after stimulation, CD was able to recognize the identity of the face from the very same picture shown during the stimulation.

3 | THREE KEY REGIONS FOR FIR IN THE RIGHT VOTC

All three cases briefly summarized above (KV; MB; CD) showed highly reproducible transient impairments reflecting FIR during intracerebral stimulation, both in terms of subjective reports (which usually initiate deeper experimental investigation) and quantified behavioral measures (Jonas et al., 2012; Jonas et al., 2018; Jonas et al., 2015, respectively). Subjective reports concern real faces (i.e., the faces of the clinicians or experimenters in the patient's room) and presented photographs. In all cases, a relatively large number of behavioral measures were taken outside and during DES, allowing to objectively (i.e., statistically) define the impairment relative to trials without stimulation or stimulation to noneloquent electrode contacts. Taken together, these

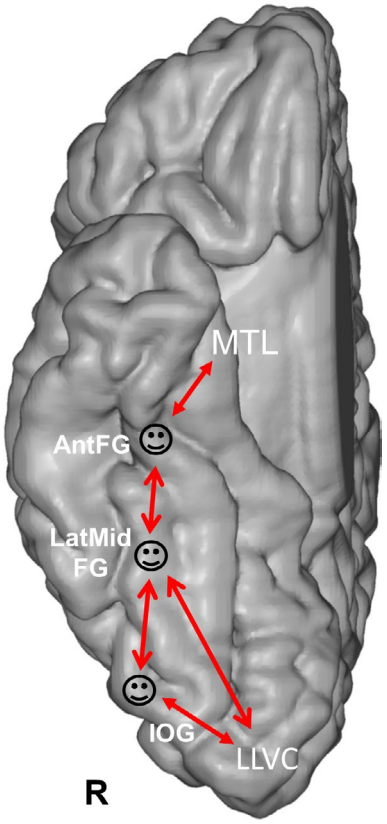

FIGURE 4 Schematic illustration of the localization of 3 key regions for human FIR (right IOG, LatMidFG and AntFG) based on DES, and of their hypothetical patterns of connectivity. Key regions are shown at their approximate locations—considering a wide interindividual variability—as schematic faces on a reconstructed cortical surface of the Colin27 brain. Transient changes of the currently experienced face stimulus during DES of the right IOG and LatMidFG would be due to reentrant direct connections between these face-selective posterior regions and low-level (i.e., retinotopic) visual cortex (LLVC). In contrast, the face-selective AntFG is not directly connected to the LLVC, but has direct connections with the medial temporal lobe (MTL), mainly the hippocampus, such that stimulation of the AntFG leads to transient failures to encode the visual stimulation experience in memory. In line with the unilateral observations made on the three cases reported, only regions of the right hemisphere are depicted here, although there is no evidence against a similar, complementary, neurofunctional organization in the left hemisphere, with a less significant contribution to FIR in most individual brains

stimulation studies point to critical regions for FIR being distributed in the right VOTC, from the occipital lobe to the posterior section of the ATL (Figure 4).

As indicated earlier, many fMRI-adaptation studies reported face identity effects in the *bilateral* IOG and LatMidFG but did not inform about the critical role of these regions in FIR. The presently reviewed DES studies suggest that the IOG and LatMidFG regions lateralized to the right, but not the left hemisphere, may be *necessary* for FIR. Moreover, the lack of reported effects following

DES in corresponding regions of the left hemisphere (despite a proportionately larger exploration and stimulation of this hemisphere in SEEG epilepsy studies; e.g., Hagen et al., 2020), suggests that the right hemisphere is *sufficient* to support the FIR function. Although this conclusion does not imply that the left hemispheric regions do not contribute to FIR in most individual brains, it is consistent with lesion studies of prosopagnosic patients, showing bilateral or right unilateral VOTC lesions (Meadows, 1974; Bouvier & Engel, 2006; Barton, 2008; Cohen et al., 2019; see Rossion, 2014 for review). So far, to our knowledge, only a handful of cases of prosopagnosia with unilateral left hemispheric damage have been reported, most of them being left-handed (Eimer & McCarthy, 1999; Mattson et al., 2000), suggesting an atypical pattern of hemispheric specialization of function in these individuals (see Bukowski et al., 2013).

Importantly, SEEG DES extends the critical neural basis of FIR to the right face-selective AntFG in the ATL, a region with little evidence of relationship to FIR (although see Behrmann et al., 2007), mainly because, as in subject CD (see Figure 3b), the AntFG is affected by a strong fMRI signal drop-out making this region almost invisible for fMRI (Rossion et al., 2018; Wandell, 2011). Overall, SEEG DES observations provide evidence, beyond fMRI and lesion studies, of local critical regions for FIR in the right VOTC, extending just anteriorly to the FFA.

4 | FACE-SPECIFICITY

Along with the tests evaluating FIR, all three subjects described above also had to recognize common objects and famous scenes during DES (Jonas et al., 2018; Jonas et al., 2012, 2015; Table 1). Strikingly, stimulating the eloquent contacts for FIR never evoked a recognition difficulty for these non-face images, pointing to a face-specific recognition impairment. Moreover, subject MB (case 2) was also stimulated twice when visualizing non-face familiar images (i.e., a famous scene and a car) and did not report a perceptual mixture of non-face parts with these stimuli. Rather, MB reported seeing face-parts or faces superimposed on the images (i.e., familiar eyes superimposed on a famous scene, see Video 2, and a familiar face incorporated into the front-view of a car, with the face replacing the car mirrors; Table 1). In line with these observations, the eloquent contacts were all highly face-selective in the 3 cases, as shown by independent recordings in SEEG and fMRI (see Figures 2 and 3 for fMRI; see Jonas et al., 2012, Jonas et al., 2014 and Jonas et al., 2015 for SEEG evidence in cases KV and CD respectively). In addition, in subject MB, face-selectivity was objectively quantified with a frequency-tagging approach (or Fast Periodic Visual Stimulation, FPVS; Jonas et al., 2016; Rossion et al., 2015): among the 138 recording contacts implanted in the subject's brain, the eloquent contact recorded the largest face-selective response (Jonas et al., 2018).

These observations suggest a tight functional link between face-selectivity and FIR. The face-selective cortical network is widely extended in primates, with a specific extension in the inferior surface of the brain in humans (Grill-Spector et al., 2017; Rapcsak, 2019; Rossion & Taubert, 2019; Sergent et al., 1992). A tentative account for this extensive face-selective network is in terms of constraints specifically imposed by FIR, that is, that a large category-selective cortical space may be required in the VOTC to achieve the particularly challenging function of face identity recognition with such efficiency, automaticity and rapidity in the human species.

5 | PRESERVED OR INTACT IMPAIRED FACE PERCEPT?

Following a standard cognitive view of the visual recognition function, and a functional distinction used to characterize visual agnosia (Lissauer, 1890; see Humphreys & Riddoch, 1987), cases of prosopagnosia following brain damage have often been defined as being either of the *apperceptive* or the *associative* type (Davies-Thompson et al., 2014; De Renzi, 1986). While a patient with apperceptive prosopagnosia is thought to be unable to build a correct visual representation of an individual face, the associative prosopagnosic patient is assumed to have a normal percept "stripped of its meaning" (Teuber, 1968). Cases KV and MB reported changes of their perceptual experience occurring during stimulation, although this was not systematic for KV. Unfortunately, due to the use of familiar faces (i.e., celebrities or clinicians/experimenters) during DES for these cases (as in all reported cases of face-related effects in ECOG; Allison et al., 1994; Mundel et al., 2003; Parvizi et al., 2012; Puce et al., 1999; Rangaranjan et al., 2014; Schalk et al., 2017; Schrouff et al., 2020), a deficit at contacting memory representations of the familiar face identity from a sufficiently preserved percept of the individuality of that face cannot be fully excluded.

A unique opportunity to test the hypothesis of an impaired visual representation of face identity independently of long-term familiarity (and of a face naming impairment) arose when KV underwent a second SEEG to perform radiofrequency-thermolesions of the epileptic focus (Jonas et al., 2014). An intracerebral electrode was again inserted in KV's right IOG, near the location of the initial exploration (Figure 2b). A behavioral paradigm with simultaneously presented pictures of *unfamiliar* faces was designed to test this hypothesis. Two identical or different unfamiliar face identities were presented next to each other at each

trial, asking subject KV to determine whether the faces were of the same identity or not (Figure 2b). To adjust the task to the KV's excellent FIR ability (according to extensive neuropsychological tests), faces that differed only by 40% along a morphed continuum were selected. While KV performed this task extremely well outside of stimulation, DES inside the face-selective right IOG led to systematic errors (i.e., answering "same" when different unfamiliar face identities were presented, Video 4, Table 1). She stated: "I saw the faces, I had a feeling of a strong resemblance", "for me, there were two identical faces". It is as if DES inside the right IOG interrupted her ability to grasp the physical differences between the two unfamiliar face identities. There was no visual distortion or rearrangement of facial elements reported. These results were supported by independent electrophysiological recordings evaluating the sensitivity to unfamiliar face identity with FPVS adaptation (Rossion & Boremanse, 2011, Figure 2b). Strikingly, among all electrode contacts implanted in KV's brain ($N = 27$), the largest repetition suppression effect for individual faces was again recorded on the eloquent stimulation site (Figure 2b).

Although subject MB (case 2 described above) was not tested behaviorally with unfamiliar faces during DES, the sensitivity to unfamiliar face identity of each contact was also measured, this time with a FPVS face individuation oddball paradigm (Liu-Shuang et al., 2014; Rossion et al., 2020). Again, of all the 137 recorded contacts, the eloquent contact in the right LatMidFG recorded, by far, the largest neural face individuation response (Figure 3a).

These last observations support the view that DES in the right IOG and LatMidFG interrupts the ability to pick out the visual idiosyncratic features that make every face unique, independently of the (long-term) familiarity of the faces. Since the third case, CD, was not tested with unfamiliar faces and did not experience any change of percept during DES, it may be that her transient FIR impairment corresponds to a true case of associative prosopagnosia, which has been related to ATL damage (Davies-Thompson et al., 2014). However, such brain-damaged patients usually present with multimodal person identity recognition deficits rather than prosopagnosia per se (e.g., Sergent & Poncet, 1990; see Gainotti, 2013). Moreover, providing that they are stringently tested, apparent cases of associative prosopagnosia systematically present with difficulties even at discriminating simultaneously presented pictures of unfamiliar faces, these difficulties being often expressed in terms of prolonged response times (Davidoff & Landis, 1990; Delvenne et al., 2004). To address this issue, future DES in the (right) AntFG will have to test for person identity recognition beyond faces, and record both accuracy rates and response times during simultaneous matching tasks of unfamiliar faces. Ideally, independent electrophysiological measures of unfamiliar face individuation with FPVS-SEEG should also be carried out.

6 | FUNCTIONAL DIFFERENCES AND SIMILARITIES OF THE 3 KEY REGIONS FOR FIR

The behavioral effects of electrical intracerebral stimulation summarized in three cases here are usually restricted to (bipolar) stimulation of one pair of electrode contacts with, more rarely, an effect also observed on a contiguous pair. Importantly, this does not imply that the effect observed is due to the sole interruption of neural activity in the stimulated local region. Indeed, DES can lead to disruption of neural processes away from the stimulated contact, especially in regions that are directly anatomico-functionally connected to the stimulated region (Borchers et al., 2012; Penfield, 1958). Face-selective regions of the VOTC, especially the IOG and LatMidFG are thought to be highly connected by white matter fiber tracts (Gschwind et al., 2012; Maher et al., 2019; Pyles et al., 2013; Weiner & Zilles, 2016) probably carrying reentrant inputs between these regions (Duchaine & Yovel, 2015; Haxby et al., 2000; Rossion, 2008).

Stimulating the posterior face-selective regions with SEEG (IOG and LatMidFG) often evoked perceptual changes (facial elements in disarray, seeing the different faces as being the same, facial palinopsia, Table 1). This observation is in agreement with ECOG DES studies consistently reporting facial perceptual changes (usually a perceptual distortion) when stimulating the right LatMidFG (Parvizi et al., 2012; Rangaranjan et al., 2014; Schalk et al., 2017; Schrouff et al., 2020; Sanada et al., 2021; see also Mundel et al., 2003). In contrast, as noted above, DES inside the right AntFG did not evoke perceptual effects (case 3, CD, Table 1). At first glance, and considering that only three cases have been reported so far, this contrast could be tentatively interpreted as functional differences between critical regions for FIR, with posterior regions involved in the construction of a visual representation of the face identities and more anterior (i.e., ATL) regions holding memory representations of these identities. Again, this interpretation would be in agreement with the apperceptive/associative distinction of prosopagnosia and with a sharp functional dissociation as advocated in neurocognitive models of face processing between a "structural encoding stage" and a store of "facial recognition units" (Bruce & Young, 1986; Calder & Young, 2005; Duchaine & Yovel, 2015; Haxby et al., 2000). However, stimulations of the right IOG evoking a FIR impairment in KV were not systematically associated with perceptual changes (Jonas et al., 2012). Moreover, SEEG recordings in a large population of individuals show that all of these 3 regions, including the right AntFG, are strongly sensitive to high-level visual discrimination of *unfamiliar* faces (Jacques et al., 2020). Considering also the above-mentioned limitations of a sharp distinction between apperceptive and associative

prosopagnosia in neuropsychology (see also Farah, 1990), we propose instead that differences in DES-evoked FIR effects across face-selective regions of the right VOTC could be accounted for by differences in their relative patterns of anatomico-functional connectivity (Figure 4). More specifically, posterior face-selective regions would have direct reentrant with low-level (i.e., topographical) visual areas in the occipital lobe (Gschwind et al., 2012; Maher et al., 2019; Pyles et al., 2013; Weiner & Zilles, 2016) so that the stimulation current during DES would monosynaptically propagate to these areas, leading to changes of the currently experienced stimulus (i.e., a perceptual change). In contrast, the AntFG does not directly connect with low-level visual areas, but with the medial temporal lobe/hippocampus (Catenoix et al., 2011; Kahn et al., 2008; Libby et al., 2012; Zhang et al., 2016). This would tentatively explain why subject CD, after intracerebral stimulation, was unable to remember even having been presented the faces, as if this episode had never entered her memory (Video 3, Jonas et al., 2015).

Even though face-selective regions of the right IOG and LatMidFG (i.e., OFA and FFA) are thought to be highly connected and DES effects could propagate across the 2 regions, one could still expect relative differences in behavioral impairments between the stimulation of these two cortical regions. Indeed, neurofunctional models of human face recognition have often associated the most posterior region (IOG/OFA) to the early perception of independent facial features essentially for the purpose of face detection, while the more anterior region (LatMidFG/FFA) would rather be involved in coding face identity holistically (Duchaine & Yovel, 2015; Haxby et al., 2000). However, it is fair to say that these neurofunctional distinctions do not rest on solid evidence and are contradicted by several observations. For instance, in the same individuals, TMS to the OFA may leave face detection intact but impair FIR (Solomon-Harris et al., 2013), while impairment of face detection in ECOG studies has rather been described following (right) LatMidFG stimulation (Chong et al., 2013; Keller et al., 2017). Moreover, there is no direct evidence of part-based face-selective representations in the human brain, a part-based processing mode being rather characteristic of cases of prosopagnosia following brain damage; see, for example, Sergent & Signoret, 1992; Van Belle et al., 2010). More fundamentally, such hierarchical neurofunctional views cannot account for rapid face detection based on holistic representations (e.g., Mooney faces) recruiting preferentially face-selective regions of the right LatFG (Rossion et al., 2011).

Since there was no systematic distinction between perceptual changes evoked by the stimulation of the right IOG and LatMidFG, the investigations reviewed here, admittedly limited to two cases (3 reports), do not provide further support for such hypothetical hierarchical neurofunctional views. For example, stimulation of the right IOG in KV evoked effects that could be tentatively linked to impairment of part-based processes (i.e., facial features being displaced) or holistic/configural perception of faces (i.e., global impression that different faces looked the same, or inability to perceive the face as a whole; Jonas et al., 2012; Jonas et al., 2014). In the same vein, stimulation of the right LatMidFG in MB could equally be interpreted either in terms of part-based representations (i.e., facial parts evoked to combine with the parts of the currently viewed facial identity) or holistic representations (i.e., seamless perceptual integration of a facial part into a unified facial representation). Moreover, as mentioned above, DES performed with well-controlled face identity tasks and independent SEEG electrophysiological recordings showed that both the right IOG and LatMidFG are involved in the ability to pick out the visual idiosyncratic features that make every face unique (Jonas et al., 2014, Jonas et al., 2018). Finally, at the temporal level, a face-selective N170 was recorded at the eloquent sites in the right IOG (Jonas et al., 2012, 2014; see also Jacques et al., 2019 for a detailed study of the N170 recorded in the right IOG of KV's brain), showing that this region is not restricted to the early stage of face processing and shows face-selectivity in the same time-window as the LatMidFG (Allison et al., 1999; Mundel et al., 2003; see also Barbeau et al., 2008).

In summary, with the current available evidence, SEEG DES studies do not support the view that these two posterior regions of the cortical face-network contribute differently to face (identity) recognition and would be involved at fundamentally different time-windows. Yet, in order to induce a FIR impairment when stimulated, the 3 key regions may share specific neurofunctional characteristics that distinguish them from noncritical FIR regions. For instance, besides their highly face-selectivity, they may have a higher pattern of connectivity compared to noncritical FIR regions, which provides these nodes to be input gates into a larger network supporting FIR (Mandonnet et al., 2010). This hypothesis is supported by DES studies revealing that critical cortical sites for language-related functions are highly connected within the language-related network and show stronger connectivity than noncritical sites (Perrone-Bertolotti et al., 2020; Rolston & Chang, 2018). According to this hypothesis, thanks to their high connectivity, stimulating critical FIR nodes will lead to the stimulation current physiologically propagating to the whole (or a large part at least) of the FIR network, inducing a behavioral effect. This hypothesis provides to reconcile two main observations: on the one hand a large and widely distributed network supporting FIR responses across the VOTC (Jacques et al., 2020) and, on the other hand, the observations of (so far) "only" 3 critical regions identified among this distributed network.

7 | WHAT IS THE ROLE OF THE LEFT HEMISPHERE IN FACE RECOGNITION?

In the human brain, the dominance of the right hemisphere in face recognition mentioned at the beginning of the present review has been supported for decades by evidence collected with a variety of methods (lesion studies, divided visual field presentations, Positron Emission Tomography, fMRI, EEG, TMS, SEEG etc.) and is undisputed. However, there is no agreement about the factors subtending this hemispheric lateralization of function, with different hypotheses having been proposed: a right/left hemispheric imbalance in holistic/analytic visual processes (Bradshaw & Nettleton, 1981; Farah, 1990), or in sensitivity to low- versus high-spatial frequencies of the sensory inputs (Sergent, 1985) respectively, or else a neural competition with language-related representations in the left hemisphere taking cortical space and therefore driving the lateralization of face representations to the right hemisphere (Ellis, 1983; see also Corballis, 1991; Dehaene et al., 2010; Berhmann & Plaut, 2015).

In the early ECOG studies reporting transient inability to name pictures of famous faces, this effect was found more often during stimulation of the left than the right fusiform gyrus (Allison et al., 1994; Puce et al., 1999). However, the relative number of stimulated sites and their degree of face-selectivity may not have been matched between the two hemispheres. Moreover, a potential disruption of access to face names rather than a visual recognition impairment per se could not be excluded. In contrast to these early observations, perceptual changes in more recent ECOG studies have been found following DES almost exclusively in the right hemisphere (Mundel et al., 2003; Parvizi et al., 2012; Schalk et al., 2017; Schrouff et al., 2020; see Rangarajan et al., 2014 for a systematic comparison of the left and right LatMidFG; see Rangarajan & Parvizi, 2016 as well as Sanada et al., 2021 for rare effects in the left LatMidFG of a left-handed subject in each study). In our own investigations, despite DES being routinely performed in corresponding regions of the left and right hemispheres, impairments of FIR following VOTC stimulation were found so far only in the right hemisphere, as reviewed here. Overall, the right hemispheric dominance of face-related effects in DES studies is therefore very clear (see also Vignal et al., 2000 for face perceptual changes during right prefrontal intracerebral stimulation).

With respect to the lateralization of function, this imbalance across hemispheres in DES studies does not rule out a role of the left hemisphere in face (identity) recognition and does not provide any evidence for qualitative rather than quantitative differences between the two hemispheres at this function. However, it is in line with evidence from cases of prosopagnosia following brain damage, as discussed above, that the right hemisphere is both sufficient (i.e., to compensate for transient interruption of function in the left hemisphere) and (in some cases) necessary for face identity recognition (so that DES to the right hemisphere alone can sometimes completely disrupt the function). Moreover, in relation to the point addressed in the previous section, this hemispheric imbalance shows that the effect of DES does not spread indifferently across the whole *bilateral* cortical face network.

8 | A SEEG ADVANTAGE IN EVOKING FIR IMPAIRMENTS?

Up to now, despite regularly applying DES inside the LatMidFG and AntFG over the last 10 years in clinical routine (with only few stimulations in the more rarely implanted IOG), our research team only observed 3 cases so far with such transient FIR impairment in SEEG. In comparison, changes of perceived face stimuli have been more frequently reported with DES in ECOG (Mundel et al., 2003; Parvizi et al., 2012; Rangarajan et al., 2014; Sanada et al., 2021; Schalk et al., 2017; Schrouff et al., 2020). While this difference could be merely due to the wider use of ECOG as compared to SEEG in clinical investigations of epileptic patients refractory to medication, there might be other reasons behind this difference in the number of reports.

First, with the exception of early studies (Allison et al., 1994 and Puce et al., 1999) and the case reported by Parvizi et al., (2012) who was not impaired at naming famous face pictures, ECOG DES studies with face stimuli essentially required subjects to passively look at faces (Mundel et al., 2003; Rangarajan et al., 2014; Rangarajan & Parvizi, 2016; Sanada et al., 2021; Schalk et al., 2017; Schrouff et al., 2020) or to perform face detection tasks (Chong et al., 2013; Keller et al., 2017), without specifically testing for FIR impairment.

Second, compared to the relative low risk profile associated with the small burr holes of SEEG, ECOG requires a full craniotomy. This heavier procedure does not only lead to more surgical complications in ECOG than SEEG (Cardinale et al., 2012; Yan et al., 2019) but is also likely to leave the subject less alert cognitively to accurately report his/her perceptual experiences and to perform explicit behavioral tasks during DES.

Finally, spatial sampling of SEEG is narrower that ECOG, reducing the chance to fall on a critical spot for FIR. In return, thanks to lower intensity stimulation (1 to 2 mA), smaller intercontact spacing (1.5 mm edge-to-edge, 3.5 mm center-to-center) (Figure 1), and to the position of the electrodes embedded inside the cortex rather than onto the cortical surface, SEEG allows for more focal stimulation than ECOG. Therefore, ECOG stimulation probably involves a relatively large cortical zone beyond regions specifically involved in

FIR, explaining global distortions of the faces (prosopometamorphopsia) sometimes also for non-face objects (Parvizi et al., 2012; Rangarajan et al., 2014), face-related effects when stimulating non face-selective sites (Schrouff et al., 2020; see also Puce et al., 1999), or impairment at a coarser level (face detection, Chong et al., 2013; Keller et al., 2017). In contrast, focal stimulation with SEEG may provide to more specifically disturb the function of a local population of neurons critically involved in FIR.

9 | CONCLUSIONS AND PERSPECTIVES

As illustrated in Figure 4, the SEEG DES studies reviewed here point to at least 3 regions critical for FIR in the human brain: the right IOG, LatMidFG and AntFG, with the latter usually "invisible" in fMRI due to a large magnetic susceptibility artifact. Independent electrophysiological recordings show that these critical stimulation sites, as well as these regions in larger populations of individual brains sampled, are highly sensitive to FIR. Up to now, even though relatively recent human fMRI studies have identified face-selective responses in more anterior ATL regions, up to the temporal pole (e.g., Rajimehr et al., 2009; Rossion et al., 2012; Axelrod & Yovel, 2013; Pyles et al., 2013; Collins et al., 2016; Kovács, 2020), there has been no evidence through DES that these anterior ATL regions critically and specifically contribute to FIR.

Even if populations of neurons sensitive to face identity are widely distributed along the bilateral human VOTC (Jacques et al., 2020), and this large cerebral network may be needed for FIR to be achieved with such efficiency (Sergent et al., 1992), SEEG DES reports indicate that a few local regions hold specific characteristics such that when their function is disrupted by focal electrical stimulation, FIR is transiently impaired. Based on the presently reviewed observations, these characteristics can be summarized as follows: (1) the critical regions are located in the VOTC of the right hemisphere; (2) they are at the heart of the cortical face network, showing the highest neural face-selectivity response; (3) they are associated with the highest neural measures of sensitivity to the visual individuality of the faces independently of long-term face familiarity; and (4) they may have higher anatomico-functional connectivity compared to non-critical FIR regions.

DES studies are sometimes considered as "anecdotal" (e.g., Schrouff et al., 2020), mainly because of limited testing time due to clinical constraints. While taking into account these constraints, future DES studies should nevertheless attempt to "bring the experimental lab in the patient's room" (Chong et al., 2013; Jonas et al., 2014; Keller et al., 2017), linking different electrophysiological measures to a variety of behavioral tasks (e.g., requiring visual discrimination beyond naming), stimuli (familiar and unfamiliar faces, non-face stimuli), and variables (i.e., response times in addition to accuracy measures), across a wide number of subjects and brain regions. Ideally, these tasks should be evaluated before DES as part of a stringent neuropsychological evaluation, to ensure that the epileptic subjects tested have a well preserved FIR function (Volfart et al., 2020). By adopting a more extensive and stringent experimental approach, further DES studies will not only inspire but also constrain and help developing our theoretical framework of human face recognition.

10 | VIDEOS

Four videos of the effect of stimulation are available in supplemental material.

CONFLICT OF INTEREST

The authors have no conflict of interest to declare. The studies described in detail in the review were all approved by the Ethical Committee of the CHRU Nancy, with written consent provided by the tested subjects. The data reviewed of the four stimulation studies reviewed here are available upon reasonable request to either of the two authors.

AUTHOR CONTRIBUTIONS

JJ was directly involved as experimenter in the four stimulation studies reviewed, and BR in two studies (Jonas et al., 2014; Jonas et al., 2018). Both authors wrote the manuscript and equally contributed.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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