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REVIEW

Mapping face categorization in the human ventral occipitotemporal cortex with direct neural intracranial recordings

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The neural basis of face categorization has been widely investigated with functional magnetic resonance imaging (fMRI), identifying a set of face-selective local regions in the ventral occipitotemporal cortex (VOTC). However, indirect recording of neural activity with fMRI is associated with large fluctuations of signal across regions, often underestimating face-selective responses in the anterior VOTC. While direct recording of neural activity with subdural grids of electrodes (electrocorticography, ECoG) or depth electrodes (stereotactic electroencephalography, SEEG) offers a unique opportunity to fill this gap in knowledge, these studies rather reveal widely distributed face-selective responses. Moreover, intracranial recordings are complicated by interindividual variability in neuroanatomy, ambiguity in definition, and quantification of responses of interest, as well as limited access to sulci with ECoG. Here, we propose to combine SEEG in large samples of individuals with fast periodic visual stimulation to objectively define, quantify, and characterize face categorization across the whole VOTC. This approach reconciles the wide distribution of neural face categorization responses with their (right) hemispheric and regional specialization, and reveals several face-selective regions in anterior VOTC sulci. We outline the challenges of this research program to understand the neural basis of face categorization and high-level visual recognition in general.

Keywords: face categorization; human brain; intracerebral; SEEG; fast periodic visual stimulation

Introduction

Recognizing individual people by their face and decoding, for example, their emotional expression and gender from facial signals is critical for social interactions. These functions rely first and foremost on the brain's ability to categorize faces as faces, that is, to discriminate faces from other visual signals such as nonface objects in the environment and to generalize this discrimination across widely variable exemplars of faces. The neural basis of face processing has been intensively investigated for three decades with functional neuroimaging, first with positron emission tomography[1] and then with functional magnetic resonance imaging (fMRI[2]). FMRI studies, in particular, have defined a set of regions in the ventral occipitotemporal cortex (VOTC) of the typical human adult brain responding significantly more to pictures of faces than nonface objects even when no explicit categorization task is required. These *face-selective* regions are thought to form the core of the human cortical network to process faces.[3–6] While fMRI has been the dominant player to map face-selective regions, other neuroscientific methodologies have been used. For instance, constraints from lesion studies, that is, neurological patients suffering from the loss of ability to recognize individual faces (prosopagnosia[7]), have helped better understand the functional organization of this VOTC network.[3,8]

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Among the various methods available to probe the human cortical face network, the recording of direct neural activity from intracranial electrodes implanted in epileptic patients is a long-standing technique,[9,10] which has been increasingly used in recent years. Here, we provide a critical and constructive review of the contribution of this approach to our understanding of the categorization of faces in the human VOTC. We begin by outlining the limitations of fMRI to derive a comprehensive face-selective map of the VOTC, calling for complementary direct measurements of neural activity in this region. Next, we remind the reader of the two different types of intracranial approaches and briefly summarize the findings of the studies using these approaches to understand the neural basis of face categorization. We then outline some difficulties encountered by these studies, which make their findings sometimes inconsistent with each other and with fMRI findings. Finally, on the basis of a recent large-scale intracranial study, we outline a research program to map face categorization processes in the whole VOTC on the basis of the following principles: (1) test large samples of patients in intracranial electroencephalography (iEEG) while (2) preserving individual anatomy information, and (3) rely on fast periodic visual stimulation (FPVS) to (4) objectively (i.e., a priori) define and quantify highly sensitive responses in a frequency-domain representation with minimal computational procedures.

Local fluctuations in fMRI signal strength and the lack of anterior VOTC activation

FMRI provides a sluggish and indirect (i.e., hemodynamic) measure of neural activity. For this reason, researchers often emphasize its low temporal resolution as a weakness, since fMRI provides little information about the temporal unfolding of face processes in different regions of the cortical face network. Nevertheless, time-resolved fMRI may provide information about the *relative* timing of face-selective activation in the VOTC,[11–14] supporting findings from lesion studies[15–17] and diffusion tensor imaging[17] for a nonhierarchical organization of this network.[8] In fact, at the current state of knowledge, we view the main limitation of an indirect measure of brain activity with fMRI for our object of study as being elsewhere: although reliable and meaningful fMRI measurements are made in parts of the brain that can be measured, the signal-to-noise ratio (SNR) of the neural activity recorded (i.e., the hemodynamic blood oxygenation-level dependent, BOLD, contrast) suffers from local signal variations caused by heterogeneous magnetic susceptibility of the local anatomy.[18] For this reason, the relative magnitude of the face-selective neural response cannot be fairly compared across various VOTC regions, and some of these regions (e.g., the fusiform face area, "FFA"[19,20]) may be attributed a dominant role possibly because they are relatively well spared from magnetic susceptibility artifacts.

Most importantly for our purpose, the anterior section of the VOTC is affected by a large susceptibility artifact arising from the ear canals.[18,21,22] Therefore, with conventional fMRI sequences, reliable BOLD activation is difficult to measure in this region. Several fMRI studies have located this artifact, which primarily affects the anterior half of the VOTC, between the anterior tip of the middle fusiform gyrus and the temporal pole[23–26] (Fig. 1). Consequently, fMRI studies may fail to disclose, or may underestimate, genuine face-selective responses in the anterior half of the VOTC. Most notably, face-selective activations anterior to the lateral section of the middle fusiform gyrus (i.e., the localization of the FFA) are rarely reported (Fig. 1A). Since most fMRI studies of face perception only report measures of face-selectivity in the posterior half of the VOTC, where the occipital face area (OFA) and FFA lie, the map that emerges from this research is often limited anteriorly to the middle fusiform gyrus (Fig. 1B). Hence, between 1990 and 2016, this map might have evolved from a "big blob to sharp and crisp spots" thanks to fMRI, as noted in a recent review,[20] but it did not extend anteriorly (Fig. 1C; see also Ref. 4).

Importantly, while there is growing evidence for anterior VOTC fMRI face-selective activations, in particular when using coronal slices[22] or optimized sequences for anterior temporal lobe (ATL) coverage,[27,28] these activations remain inconsistent across studies, relatively small in volume and found only in a fraction of individual brains tested (e.g., half of the subjects in Refs. 23 and 29). Most importantly, they are mostly found very anteriorly, that is, close to the temporal pole.[22,23,29–33] Thus, despite the optimization of scanning parameters, there is a gap in fMRI maps between the FFA and anterior face-selective activations close to or in the temporal pole (see the gap in Fig. 1A; see also Ref. 34 for a

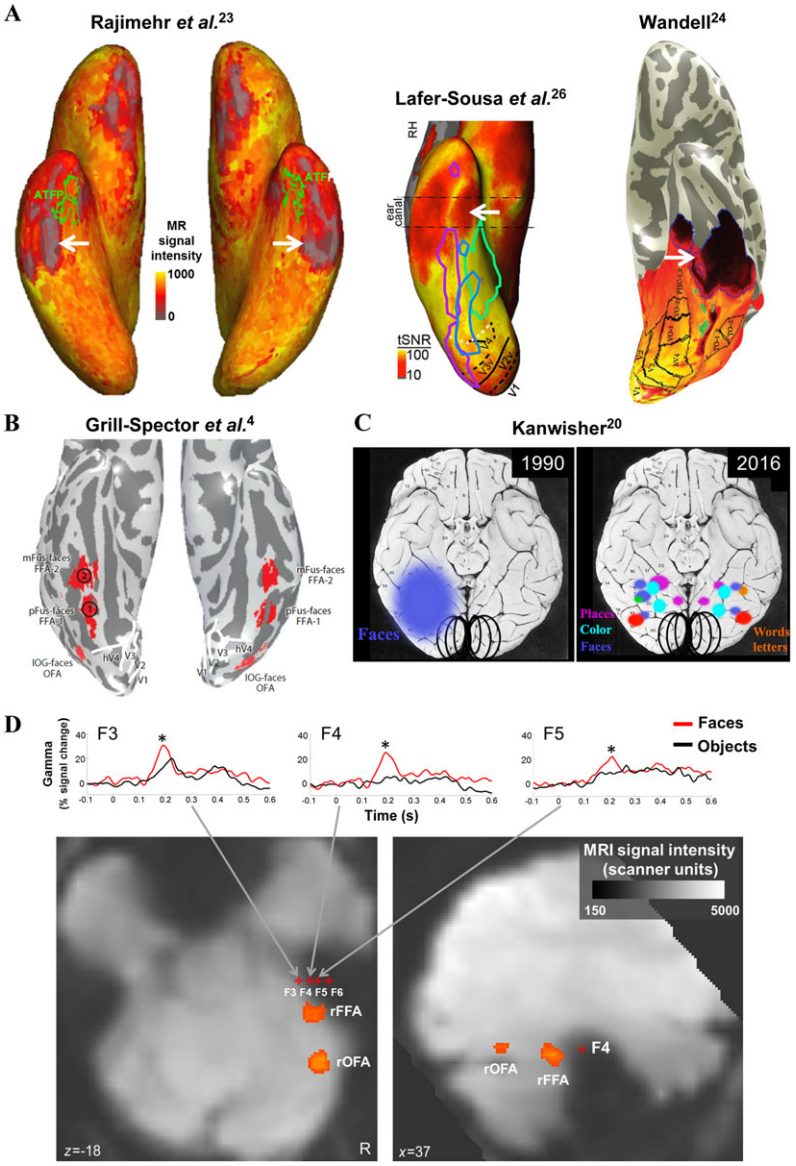

Figure 1. Magnetic susceptibility artifact due to the ear canal (or anterior VOTC signal dropout) in fMRI and its consequences on the current picture of fMRI neural basis of face categorization. (A) These examples show the BOLD signal level on ventral views of the inflated cortical surface. The anterior VOTC signal dropout is indicated by a white arrow (gray or black zone in Rajimehr *et al.*[23] and Wandell;[24] red zone in Lafer-Sousa *et al.*[26]). In these regions, BOLD measurements are not reliable. In Lafer-Sousa *et al.*,[26] the face-selective activations are indicated by purple outlines: note that face-selective activations are found all along the VOTC except in the region of the signal dropout. (B) Topological organization of the face-selective activations in the VOTC (in red) in one of the most recent reviews on the functional architecture of face perception in the VOTC.[4] Note that there are no activations anteriorly to the middle fusiform gyrus (FFA, spot indicated by "2" in the figure). (C) Schematic representation (from Ref. 20) of the progress made in the understanding of functional architecture of the VOTC between 1990 (birth of fMRI) and 2016. Although the posterior VOTC is refined, little or no progress appears to have been made in mapping and understanding anterior VOTC regions. (D) Genuine face-selective responses in the right anterior fusiform gyrus as found by intracranial recordings (top row: electrodes F3, F4, and F5) are not observed in fMRI because of the signal dropout caused by the ear canal (bottom row: fMRI face-selective areas and intracranial electrodes are shown on raw axial (left) and sagittal (right) functional slices; from Ref. 25). *Face-selective responses ($P < 0.01$). Note that this region, in the heart of the artifact, was not covered in an fMRI study using coronal slices to improve signal detection of face-selective activations in the anterior VOTC.[22]

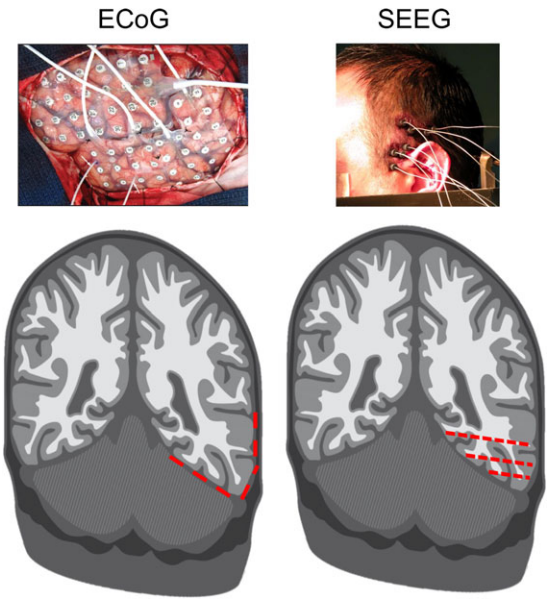

Figure 2. Intracranial (iEEG) recording techniques: ECoG and SEEG. Above, pictures of the surgical procedure involved in placing the intracranial electrodes. In ECoG, part of the skull is removed to apply electrodes onto the cortical surface (here, grids of electrodes). In SEEG, small holes are drilled in the skull to implant thin depth electrodes. Below, schematic coronal representation of intracranial electrodes in contact with the middle fusiform gyrus. The electrodes are represented in red.

meta-analysis and empirical study of anterior temporal face patches, figs. 2 and 3 of that paper).

Evidence for face-selective responses with intracranial EEG recordings

To date, the only alternative approach to provide a more comprehensive map of face-selectivity in humans is afforded by electrophysiological recordings in awake patients implanted with intracranial electrodes along the VOTC as part of their presurgical evaluation for drug-resistant focal epilepsy. These relatively rare—compared with neuroimaging—iEEG recordings allow millisecond resolution measurements of electrical fields directly associated with local neural activity. Crucially, these measurements have a high and stable SNR across VOTC regions, from the occipital pole to the temporal pole. In practice, there are two possible surgical techniques for intracranial electrode placement (Fig. 2). On the one hand, electrocorticography (ECoG[35]) consists of 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 arranged as grids or strips with typically 5–10 mm interelectrode spacing. On the other hand, stereotactic electroencephalography (SEEG[36]) consists of inserting depth electrodes within the brain, from the cortical surface to the medial cortex (i.e., *intracerebral* electrodes). The *intracerebral* electrodes are thin cylinders (e.g., 0.8 mm diameter[37]) typically containing 8–15 contiguous individual recording sites (or contacts) separated by an insulating material. From the point of view of fundamental research, both techniques have their own advantages. For example, while ECoG has the advantage of offering an extensive superficial spatial coverage, SEEG provides recordings directly inside the gray matter, allowing the specific exploration of cortical sulci and medial structures (e.g., amygdala and hippocampus). It is important to note that in both techniques, electrodes target the putative epileptogenic zone but also the surrounding normal cortex in order to assess the limits of surgical resection.

The first recordings of face-evoked potentials in the human VOTC were reported in the 1990s by Allison and colleagues[9] at Yale using ECoG and Halgren and colleagues[10] working in Paris and Rennes with SEEG. Allison *et al.*[9] recorded a negative potential larger for pictures of faces than objects, the N200, over the posterior and anterior sections of the fusiform gyrus, and the inferior occipital gyrus (IOG). This work provided the impetus for the subsequent recording of the face-selective N170 over the human scalp of typical individuals with the same paradigm and stimuli.[38] Subsequently, the Yale research team published three seminal papers, reporting ECoG recordings performed in 98 patients over the ventral and lateral occipitotemporal cortex.[39–41] Face-selective N200s were recorded over the fusiform gyrus (as in Allison *et al.*,[9] Fig. 3A) and a later additional face-selective potential (AP350) located anteriorly to the N200 in the ATL (Fig. 3A). More precisely, this AP350 potential was located over the anterior fusiform gyrus, the anterior inferior temporal gyrus, and the temporal pole, with a right hemispheric dominance.

Using SEEG, Halgren *et al.*[10] recorded a complex triphasic potential (N130-P180-N240) evoked by faces in the fusiform gyrus (the P180 potentially being the positive counterpart of the N200 inside the brain). They also recorded various types of

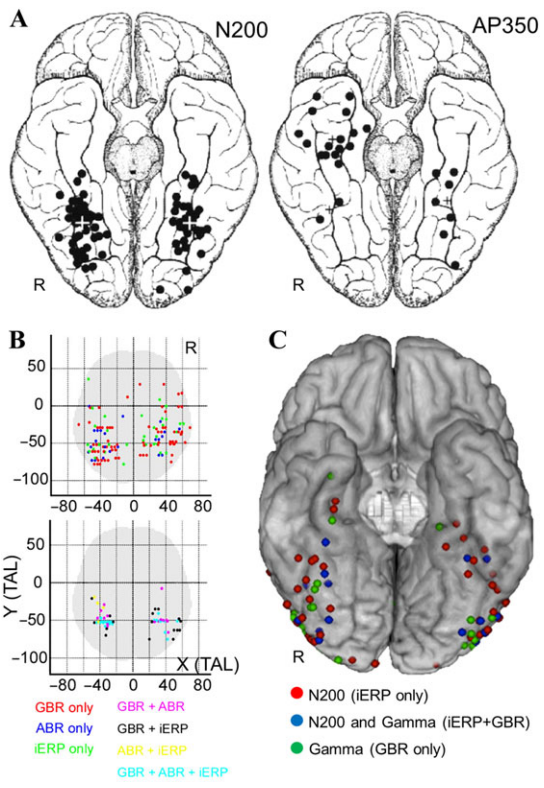

Figure 3. Spatial distribution of face-selective responses in the VOTC with iEEG. (A) Face-selective ERPs (N200 and AP350) reported in Allison *et al.*[39] (B) Face-selective responses found in Vidal *et al.*,[46] plotted in the Talairach space. Each dot represents a face-selective electrode. Electrodes are colored according to the frequency band where face-selective responses were found (GBR: gamma; ABR: alpha/beta; and iERP: event-related potentials). Note that some contacts shown here are in fact located in frontal and parietal lobes, and not in the VOTC (sagittal views not shown). (C) Face-selective responses found in Engell and McCarthy,[60] plotted in the MNI (Montreal Neurological Institute) system. Face-selective electrodes are colored according to the frequency band where face-selective responses were found.

potentials evoked by faces (varying in latency and polarity) in widespread regions of the temporal lobe (lingual gyrus, superior and middle temporal gyri, temporal pole, hippocampus, and amygdala). However, this SEEG study did not measure face-selective responses by comparing evoked responses to faces and meaningful nonface object stimuli (see also Ref. 42).

More recent studies of groups of patients of various sizes have made several important contributions for the understanding of the spatial functional organization of face-selectivity. These studies showed the predominance of face-selective responses in the lateral over the medial fusiform gyrus,[43,44] clarified the spatial relationship between face-selective and nonface category-selective responses in VOTC,[43–46] investigated the temporal dynamics of face-selective responses,[47,48] explored face-selectivity in specific VOTC regions (IOG,[49] fusiform gyrus,[50] and ventral ATL[51]), simultaneously recorded and functionally related face-selective intracranial and scalp event-related potentials (ERPs) (i.e., N200s and N170s[45]), showed the complementarity of ERPs and high-frequency broadband (HFB) activity in decoding face versus house responses,[52] or yet showed a correspondence between local iEEG and fMRI face-selective responses in posterior VOTC.[43,53,54]

The challenge of VOTC mapping with intracranial EEG recordings

Despite their interest, it is fair to say that human iEEG studies identifying face-selective cortical responses, or using face stimuli in general, have so far failed to provide a coherent map of the VOTC at a large spatial scale. Moreover, they have been largely unable to offer consistent and complementary information to fMRI studies regarding exact localization and spatial organization of face-selective responses in the VOTC. As a result, they have had little impact so far on neurofunctional models of face processing.[3,5] Let us provide three examples to support these claims.

First, larger face-selective responses are usually found in the right as compared with the left fusiform gyrus in neuroimaging[1,19,33,55] in line with brain lesion studies that have long showed a clear right hemispheric predominance of the posterior VOTC for individual face recognition (i.e., in causing prosopagnosia[8,56–58]). However, surprisingly, iEEG studies have been unable to show this right hemispheric predominance in terms of signal amplitude in the posterior VOTC, either with ERPs[39,45] or in HFB.[59]

Second, since the early work of Allison *et al.*[39] (Fig. 3A), very few iEEG studies have reported face-selective responses in the anterior VOTC.[51] This could be partly due to the dominant use of ECoG, which may be less sensitive to detect anterior VOTC face-selective responses located primarily in sulci. Perhaps for this reason, and despite good coverage of anterior VOTC regions in temporal epilepsy investigations (anterior temporal epilepsy is the most frequently investigated epilepsy

in epilepsy surgery), most iEEG studies focus on posterior VOTC[43,44,50] activity. This is unfortunate since the anterior VOTC lies precisely in the heart of the fMRI magnetic susceptibility artifact as shown earlier (Fig. 1). A recent iEEG case study showed that the anterior VOTC, in particular in between the middle fusiform gyrus and the temporal pole, may contain critical face-selective responses[25] (Fig. 1).

Third and more generally, apart from the local correspondence between iEEG and fMRI face-selective responses in the posterior VOTC,[43,53] the large-scale clustered organization of face-selective activity depicted in fMRI studies is difficult to reconcile with the mosaic distribution of face-selective responses as found with iEEG (i.e., contrast Figs. 1B and 3). Are these differences merely due to the comparison of individual maps in fMRI to group maps in iEEG, or to other trivial differences in data visualization such as comparing maps averaged across subjects in fMRI (e.g., Ref. 33) versus maps showing the superposition of all significant electrodes across subjects in iEEG (e.g., Ref. 39)? Is there truly a clustered organization of face-selective neural responses in the VOTC or are those clusters emerging in fMRI maps because they are based on a lower SNR measurement with a conservative statistical threshold? And, if clusters or peaks of activity can be found in iEEG across the whole VOTC, do they correspond to the typical locations found in fMRI (i.e., denser concentration of face-selective responses in the lateral section of the middle fusiform gyrus, FFA, or the lateral IOG, OFA)? The difficulty in addressing these issues with current sources of evidence appears to be due to a number of factors.

First, there is undoubtedly an issue of spatial sampling, with iEEG recordings remaining relatively rare despite a growing interest in the scientific community, and the localization of electrodes being determined by clinical purposes. Unlike the seminal studies cited above,[9,10,39] most studies rely on relatively small samples (e.g., $N < 10$) of individual brains and often target specific regions[48–51,59] rather than the whole VOTC.

Second, most studies with a large sample of participants (e.g., >10) combine data at the group level by normalizing individual brains into a common space (MNI or Talairach space), known to blur the individuality of functional organization (e.g., Refs. 46, 50, and 60; Fig. 3B and C). Few studies take advantage of the high anatomical resolution of iEEG studies to locate electrodes in the individual anatomy in order to group electrodes across patients (e.g., Refs. 42–44 and 47). The seminal studies of Allison and colleagues[39–41] used a combination of these approaches. Electrode locations were determined and plotted in Talairach space for the antero-posterior (y) axis and according to their gyri and sulci position as determined in individual anatomy for the mediolateral (x) and inferosuperior (y) axes.

The importance of the individual anatomy has been illustrated by fMRI studies showing that, despite the anatomical interindividual variability, some anatomical landmarks in the visual cortex can predict the location of functional visual areas (e.g., the mid-fusiform sulcus predicts the location of the face-selective activations in the fusiform gyrus;[61] the posterior transverse collateral sulcus predicts the VO1/hV4 boundary;[62] and the posterior inferior temporal sulcus predicts the location of hMT+[63]). However, grouping electrodes according to their location in individual anatomical structures across patients and across a large cortical surface (e.g., the whole VOTC) involves solving many issues such as the interindividual variability of anatomical structures, the variable ways to anatomically subdivide the brain, and the scale at which to perform this subdivision.

A third factor relates to the intracranial recording method (Fig. 2). On the one hand, ECoG allows covering an extended cortical territory but electrodes are restricted (and therefore most sensitive) to the gyral surface, further away from (and therefore less sensitive to) sulcal activity. On the other hand, SEEG covers less space on the external and gyral cortical surface but offers the opportunity to penetrate sulci and explore medial structures. In addition, ECoG and SEEG recording units have different positions relative to the cortex, which can affect the type and origin of electrophysiological signal measured.[64] Specifically, ECoG electrodes are always over the most superficial layer of the cortex, while SEEG electrodes are mostly located within the cortical sheet or at the surface of the gray/white boundary.

Fourth, the iEEG electrophysiological signal is multidimensional, varying both in time and frequency. With respect to the temporal dimension, face-selectivity can be complex to apprehend and describe, as it varies across time both within and across VOTC subregions. For instance, as

indicated above, face-selective responses are measured before 200 ms in the posterior VOTC,[39,43,47,48] and after 300 ms in anterior VOTC.[39,51] With respect to the frequency dimension, iEEG studies report increased neural activity to pictures of faces compared with nonface objects mainly in two distinct types of neural activity: (1) low-frequency responses time-locked and phase-locked to the stimulus (i.e., ERPs, such as the N200/N170 component)[9,39,45–47] and (2) high-frequency electrophysiological activity (HFB) which is often nonphase locked to the stimulus.[43,44,46,49,51,59,60,65,66] Both high- and low-frequency face-selective responses have been mainly measured in the posterior VOTC (Fig. 3). However, iEEG studies comparing these types of responses reported distinct, although overlapping spatial maps of face-selectivity[46,60] (Fig. 3B and C) and further discrepancies are found when activities in an "intermediate" frequency band are considered[46] (alpha/beta activity, from 8 to 24 Hz; see Fig. 3B). Altogether, these observations have led some authors to suggest that face-selective responses occurring in different frequency bands reflect separate, perhaps complementary processes of the face processing system,[52,60] in line with observations indicating that different frequencies reflect partly independent neural processes.[67–71] Yet, discrepancies between the spatial distributions of face-selectivity across frequency bands may also be partly due to methodological parameters. For instance, face-selective ERPs and HFB signals have sometimes been measured using different time-windows (e.g., amplitude of N200 component in ERPs versus area under the curve in a 200–600 ms time-window for HFB[60]), showing that more objective criteria for defining and quantifying face-selective responses would be welcome.

Finally, the control stimuli/categories used to define face-selective responses vary enormously across studies. In many studies, responses to faces are compared with responses to one or a few object categories without ensuring that the discrimination response is not related to confounding stimulus properties, such as differences in amplitude spectrum.[72] Most studies use 1–4 control categories, which may be too few to ensure that the face-selective response (or absence of) is generalizable.[43,45,49,51] In addition, the nonface stimuli compared with pictures of faces may be meaningless,[42] presented against a different background compared wtih faces (e.g., uniform versus cluttered background, segmented versus embedded in a visual scene;[39] difference in background luminance[48]), or have other systematic low-level differences compared with face images (e.g., face versus houses in Ref. 45). As an example of potential stimulus confound, in the studies of Allison and colleagues,[9,39] the control stimuli (cars especially) did not elicit any N200 deflection at many electrode sites, which therefore appeared as producing face-exclusive responses at the population level. However, the exact same stimuli did not evoke N170 responses on the scalp either,[38] despite the fact that the scalp N170 is typically evoked by pictures of nonface objects (in particular for cars).[73,74]

In the next section, we describe a research program that addresses these challenges specifically, in order to build an extensive cartography of the human VOTC with iEEG recordings.

A research program combining FPVS and individual anatomical localization in SEEG

Two approaches are combined in this research program. First, iEEG recordings are performed during FPVS. Second, SEEG electrodes implanted across large groups of patients are localized in individual brains using an anatomical framework across the whole VOTC. For the sake of simplicity, we will refer to this combination as the FPVS-SEEG approach.

Fast periodic visual stimulation to define face-selectivity

Face-selective neural responses are measured by presenting natural images of objects at a fast rate of six images by second (Fig. 4A, movie 1; from Ref. 75). The stimulation runs continuously for about 1 min, and the subject does not explicitly categorize the images, simply maintaining fixation on a central cross and detecting its 6–8 times random changes of color. A Fourier transform of the whole minute of (S)EEG recording reveals peaks of neural activity in the amplitude spectrum, exactly at the stimulation frequency F, that is, 6 Hz, and its harmonics (2F = 12 Hz, etc.; Fig. 4B). With this paradigm, such frequency-tagged responses are readily (i.e., with minimal computational steps) identified both on the scalp[75–77] and inside the human brain.[78]

The property of the human brain to synchronize its activity to a flickering light is a fairly old observation in scalp EEG[79] (see Ref. 80 for an early

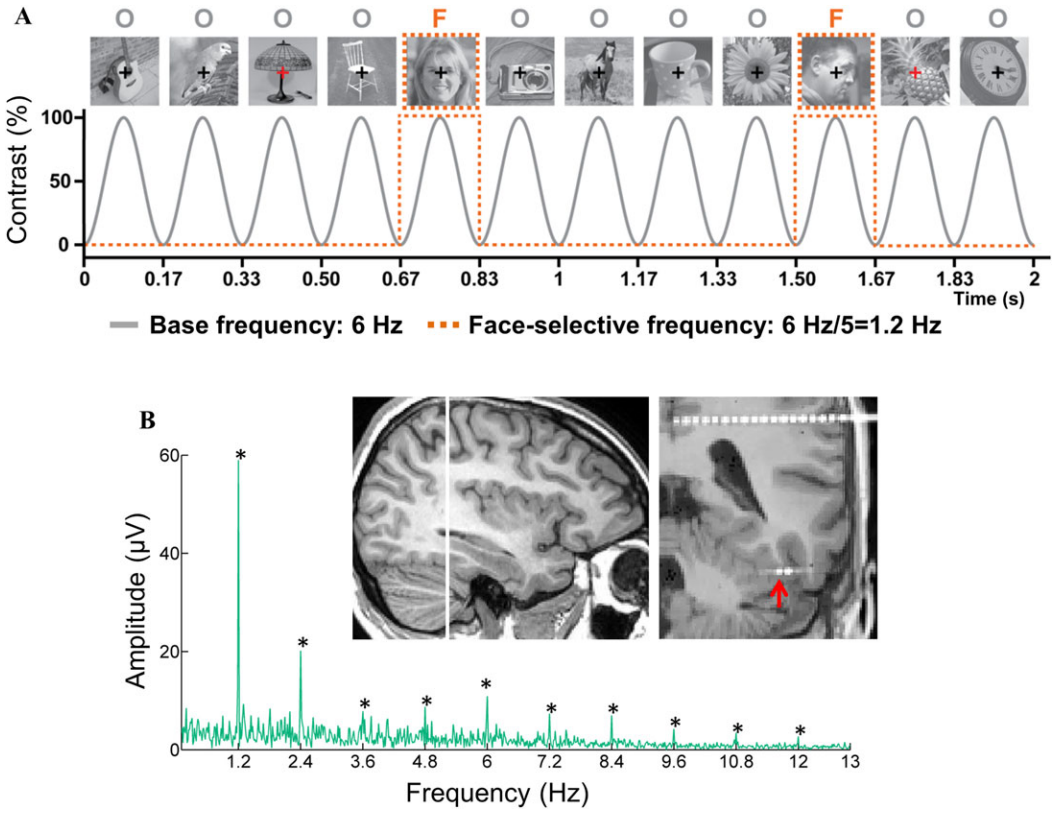

Figure 4. Experimental FPVS paradigm and example of a face-selective response recorded on a single electrode contact in the fusiform gyrus (from Ref. 78). (A) The FPVS paradigm. Images of objects are presented by sinusoidal contrast modulation at a rate of six stimuli per second (6 Hz), with a different face image presented every five stimuli (i.e., appearing at the frequency of 6 Hz/5 = 1.2 Hz). (B) Objective and high SNR intracerebral responses in the VOTC of a single individual brain. IEEG frequency-domain responses recorded at an individual recording contact (raw FFT amplitude) located in the right latFG are shown. The location of the recording contact (indicated by a red arrow) is shown using a postoperative CT coregistered to a preoperative MRI. Significant face-selective responses exactly at the face-selective frequency (1.2 Hz) and harmonics (up to 10.8 Hz) are observed. *Statistically significant responses ($Z > 3.1$, $P < 0.001$).

use of the approach in intracranial recordings). Regan[81] used a Fourier analyzer to show that EEG responses recorded in these conditions at various frequency rates could be expressed in the frequency domain as narrow peaks of activity exactly at the frequency of stimulation with extremely high SNR (see Refs. 82 and 83 for reviews). Here, the original and critical aspect of the approach is to present *variable* complex stimuli at each stimulation cycle. Moreover, a second frequency of interest is generated by inserting pictures of faces—also widely variable and nonsegmented from their natural background (Fig. 4A)—every five stimuli. Hence, an EEG response at 6 Hz/5, that is, 1.2 Hz, reflects a selective (i.e., differential) response to faces, which translates as a 1.2 Hz peak of activity in the frequency spectrum, with corresponding harmonics (2.4 Hz, etc.; Fig. 4B). Crucially, a population of neurons responding identically to faces and nonface objects will be reflected in the common 6 Hz response, and not in the 1.2 Hz response. Hence, a response at 1.2 Hz and its harmonics (excluding 6 Hz) does not only reflect a face-evoked response, but also directly a *face-selective* response.[75,84]

This relatively simple approach has many strengths, making it a unique tool for understanding face categorization in the human brain, particularly with iEEG.

First, it is associated with an extremely *high SNR*, providing significant responses even on the scalp

within a few minutes of recording.[45,76,84] This high SNR is mainly due to the very high frequency resolution obtained by analyzing a single long sequence of stimulation (e.g., 0.016 Hz, i.e., 1/60 s). Thanks to this high frequency resolution, while the SEEG noise is distributed across many frequency bins, the signal of interest projects to a single tiny bin (i.e., of 0.016 Hz) associated with very little noise.[82] This offers considerable advantages over other stimulation approaches using slow rate transient nonperiodic events. In particular for iEEG, this approach can be highly resistant to epileptic spikes, which are very large deflections (several hundreds of μV), sometimes occurring repeatedly throughout the recordings.[85] These spikes increase the general noise level, and in the case of a transient stimulation paradigm can lead to the rejection of a large number of trials containing epileptic spikes, therefore resulting in a reduced amount of reliable data or in the increase in the experiment duration. In a group study detailed below,[78] it can be shown that the results are virtually identical with or without an artifact rejection step (i.e., epileptic spikes rejection). Obviously, this high SNR affords short recording sessions, which is particularly important in iEEG studies with epileptic patients in a clinical setting.

Second, this paradigm provides a *valid* measure of face categorization. That is, instead of measuring the response to one type of stimulus and another type of stimulus separately, it aims at measuring the *process* of face categorization, which involves direct *discrimination* (between faces and nonface objects), and *generalization* of this discrimination across widely variable images. Indeed, a significant face-selective response in this paradigm emerges only if there is a response at most face stimuli, thus ensuring generalization across a widely variable set of images. For instance, a population of neurons responding only to full front faces would respond only once in the short example of 2 s illustrated in Figure 4A, and thus not contribute to a 1.2 Hz response. Moreover, faces need to elicit a differential brain response to the various object categories presented in the sequence, and not just one type of object. For instance, a population of neurons responding selectively to living things will fire four times over 2 s as shown in the example provided in Figure 2, breaking the periodicity. Hence, the paradigm does not merely measure an average response to faces as compared with an average response across the nonface object categories. Thanks to the same periodicity constraints, the face-selective response is not contaminated by low-level visual cues that would have to be systematically, that is, periodically, associated with faces and never or rarely associated with nonfaces to generate a low-level 1.2 Hz response. Therefore, the approach provides control by variability rather than by elimination/homogenization. This has been shown in scalp EEG studies, showing that phase-scrambling of the stimuli eliminates face-selective occipito-temporal responses.[75] Of course, this is only true if a wide variety of images belonging to different categories are used (see fig. 1 in Rossion *et al.*[75] and stimuli available here: http://face-categorization-lab.webnode.com/resources/natural-face-stimuli/).

Finally, the response of interest can be identified in the frequency domain objectively, that is, exactly at the frequency of stimulation determined a priori by the experimenter.[82] Quantification is performed by summing the harmonics related to the frequency of interest, corrected for noise level by subtracting the activity in the neighboring frequency bins.[84] This leads to a relatively straightforward and replicable data analysis procedure that provides a common systematic metric to estimate face-selectivity across brain regions, studies, and methodologies (i.e., ECoG and SEEG). Note that with this frequency-domain representation, face-selectivity here is not restricted to a *larger* response to faces than objects but to a systematically *distinct* neural response to faces. Indeed, a population of neurons responding significantly *less* to faces than to all other object categories, hence providing a strong signal to the brain that a face is present in the visual environment, will lead to a 1.2 Hz face-selective response in this paradigm. Moreover, a population of neurons responding with the same magnitude overall to faces and objects, but systematically earlier or later, or with a different shape of response, to faces than all other images should also lead to a 1.2 Hz response in this paradigm. Hence, the frequency-domain representation captures a full selective response to faces, making no assumption as to the form and properties of the face-selective response.

SEEG and electrode location in the individual anatomy

The problem of spatial localization of responses is addressed by labeling each individual recording

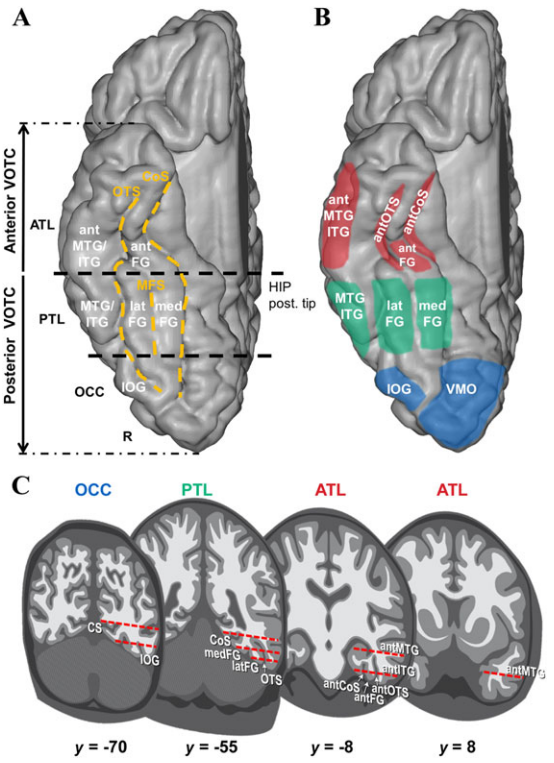

Figure 5. Individual anatomical localization of SEEG electrodes. (A) Example of a VOTC parcellation used in Jonas *et al.*[78] Major VOTC sulci served as mediolateral landmarks (CoS and OTS), and coronal reference planes containing given landmarks served as posteroanterior landmarks. A coronal plane including the anterior tip of the parieto-occipital sulcus served as the border of the occipital and temporal lobes. A coronal plane including the posterior tip of the hippocampus served as the border between PTL and ATL, and between posterior and anterior VOTC. (B) Anatomical regions that were found face selective in Jonas *et al.*[78] are highlighted in color. (C) Schematic representation of the typical trajectories of depth electrodes (SEEG) implanted in the right VOTC. Typical trajectories of electrodes are represented as arrays of red rectangles on schematic coronal slices (with Talairach *y* coordinates indicated below slices). ATL, anterior temporal lobe; PTL, posterior temporal lobe; OCC, occipital lobe; CoS, collateral sulcus; CS, calcarine sulcus; FG, fusiform gyrus; HIP, hippocampus; IOG, inferior occipital gyrus; ITG, inferior temporal gyrus; MFS, mid-fusiform sulcus; MTG, middle temporal gyrus; OTS, occipitotemporal sulcus; VMO, ventromedial occipital cortex; a, anterior; lat, lateral; med, medial.

site (contact) in the individual brain anatomy, as in previous studies.[42–44,47] The whole VOTC is subdivided in a relatively fine grid pattern,[86] with each anatomical subdivision defined by medio-lateral and posteroanterior landmarks (Fig. 5A). Using a fine anatomical subdivision allows to apprehend anatomy at multiple spatial scales by grouping anatomical partitions that show similar response properties. Importantly, the anatomical subdivision should be as much as possible independent from the interindividual variability in brain anatomy and in expertise of the experimenters in analyzing a brain MRI. Therefore, major anatomical landmarks that can be easily identified in each individual brain and by each experimenter are used. Note that an automated anatomical parcellation procedure[87] (e.g., see Refs. 44, 47, and 88) is not used, for two reasons: first, the anatomical scale at which current automatic parcellation is performed is too coarse, particularly in the anteroposterior axis; second, even when performing automated parcellation, careful verification of the parcellation is needed to avoid labeling errors.

A comprehensive definition of face-selective activity in the human VOTC

Using this approach, a first definition and quantification of face-selective responses across the whole VOTC was reported in a large group of participants ($N = 28$) implanted with SEEG.[78] Patients were selected on the basis of the presence of at least one implanted electrode in the VOTC (Fig. 5C). In the context of the present review, we summarize and illustrate the methodology and the main observations of that study, before discussing its implications in the context of a general research program.

A wide distribution of responses

Despite a brief recording time (2–4 sequences of 70 s) for each individual, face-selective responses are found in the VOTC exactly at 1.2 Hz and harmonics (see Fig. 4B for an example of recording on a face-selective contact). From a total of 1678 individual recording contacts in the gray matter of the VOTC across 28 individual brains, there were a large number of face-selective contacts (555 contacts, or 33%). These contacts were widely distributed over the VOTC, from the occipital lobe (OCC) to the ATL (see Figs. 5B, 6A, and B in the individual anatomy and Fig. 7A in the MNI space). Thus, the spatial analysis reveals a wide distribution of face-selective responses across the VOTC, in line with previous iEEG studies.[39,46] In the OCC, face-selective responses were recorded in the IOG and in a large portion of the ventral and medial occipital cortex (Figs. 5B and 7A, middle panel). In

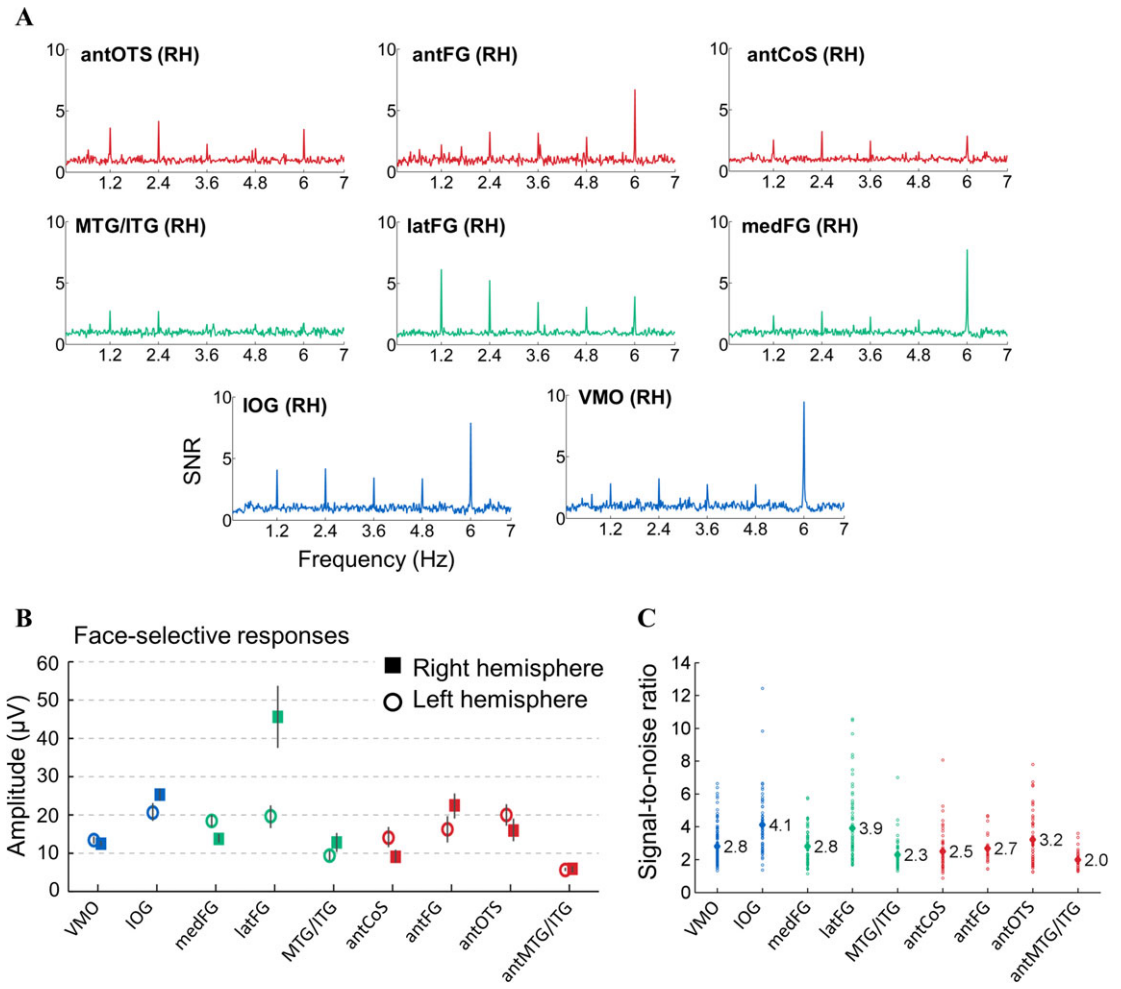

Figure 6. Face-selective responses grouped according to the individual anatomy (from Ref. 78). (A) IEEG frequency spectra in selected regions of the right VOTC averaged across all face-selective contacts located in the same region. (B) Quantification of the face-selective response amplitude in the individual anatomy. Face-selective contacts were grouped by anatomical region-of-interest across all participants and the face-selective amplitude was averaged across contacts to obtain the mean response amplitude for each region separately for the left and right hemisphere (note that this result was independent from the number of harmonics taken into account). The schematic locations of each region are shown in Figure 5B. (C) Signal-to-noise ratio (SNR) of face-selective responses in each anatomical region. Open circles display SNR for individual recording contacts and filled diamonds show the average SNR across contacts (see exact value on the right of each diamond). SNR was quantified over the first four harmonics of the face-selective frequency as follows: for each contact (1) the FFT spectrum was cut into segments centered at the face frequency (1.2 Hz) and the first four harmonics (1.2 to 4.8 Hz) and surrounded by 25 neighboring bins on each side; (2) the amplitude values of the four FFT segments were summed; and (3) the summed FFT spectrum was transformed into SNR. SNRs were computed as the ratio of the amplitude at the face frequency bin to the mean amplitude of 48 surrounding bins (25 bins on each side, excluding the two bins directly adjacent to the bin of interest).

the posterior temporal lobe, face-selective responses were recorded in the posterior fusiform gyrus, in its medial (medFG) and lateral (latFG) sections. In the ATL, face-selective responses were mainly recorded in the ventral ATL in three distinct regions: (1) along the anterior segment of the collateral sulcus or rhinal sulcus (antCoS), (2) along the anterior segment of the occipitotemporal sulcus (antOTS, located laterally to the CoS), and (3) in the anterior fusiform gyrus (antFG, located between the antCoS and antOTS, anteriorly to the posterior tip of the hippocampus). In all these regions, the mean SNR

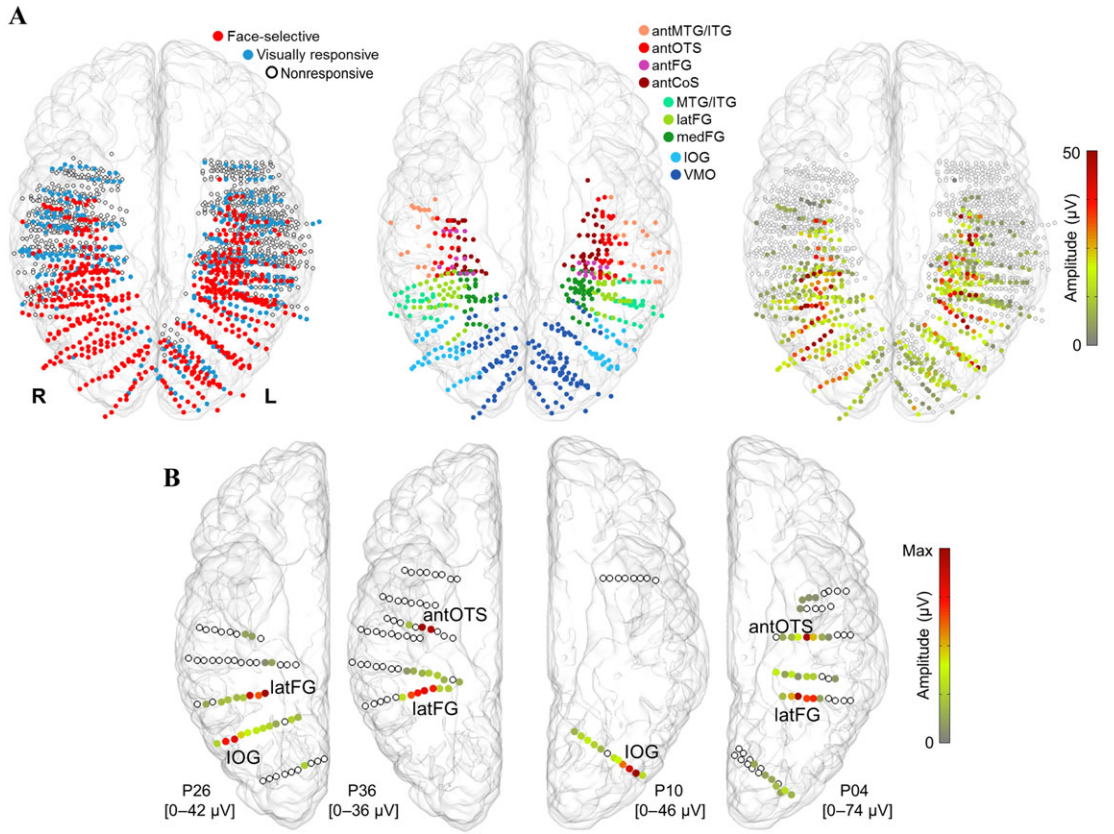

Figure 7. Spatial distribution of face-selective response across participants and in individual brains (from Ref. 78). (A) Maps of recording contacts across the group of 28 participants displayed in the MNI space using a transparent reconstructed cortical surface of the Colin27 brain. Each circle represents a single contact. Left panel: spatial distribution of face-selective, visually responsive (responsive to the base frequency but not face-selective) and nonresponsive contacts. Middle panel: face-selective contacts are colored according to their anatomical label in the individual anatomy. Note that the location of antFG contacts is blurred in the MNI space, mainly because of their proximity with the latFG, antOTS, and antCoS. Right panel: face-selective contacts are colored according to their face-selective response amplitude (white-filled circles correspond to contacts that are not face selective). (B) Examples of four individual participant hemispheres. Face-selective contacts are colored according to their face-selective response amplitude. Contacts are displayed in the MNI space, but anatomical labels of the face-selective clusters are derived from the individual native anatomy.

across contacts obtained with FPVS is very high, that is, between 2 in the antMTG and 4 in the IOG (i.e., 100–300% of signal increase; Fig. 6C).

Regional peaks of face-selectivity

To quantify face-selectivity, amplitudes are summed over harmonics for each face-selective contact,[84] and amplitude is averaged across contacts for each region. A key observation is that, across all regions, the largest face-selective response is, by far, recorded in the middle section of the right latFG (Fig. 6B). This observation therefore validates, with a direct measure of neural activity, the predominant face-selective activation in the right middle latFG found in human neuroimaging for more than two decades (i.e., the "FFA"[19]). Moreover, this finding illustrates the importance of localizing contacts in the individual anatomy. Although grouping contacts and their corresponding amplitude values in common space (MNI) showed that face-selective responses were widely distributed and more frequent in the posterior VOTC, the specific predominance of the right latFG is not readily apparent with this display (Fig. 7A, right panel). In contrast, this dominance is clear when grouping contacts according to the individual anatomy (Fig. 6B).

Distributed versus clustered spatial organization of face-selectivity

Importantly, the dominance of the face-selective response in the right middle latFG emerges by considering a relatively large group of patients and a division in relatively large anatomical regions (Fig. 5A). Hence, at a group level, the spatial resolution is relatively coarse and is inherently limited by the anatomical definition of the regions. However, at the individual level, while the sampling is limited in coverage, the spatial resolution is much higher (i.e., an intercontact center-to-center spacing is 3.5 mm with these SEEG electrodes), which affords exploring the spatial organization of face-selective responses at a finer scale within each face-selective region. Quantifying the spatial variation of face-selective response amplitude across the length of each electrode reveals that the second and third largest face-selective contacts are often contiguous to the highest face-selective contact along the same electrode (Fig. 7B), indicating a local clustering of strong face-selectivity. This observation shows that there is not a single definition of spatial resolution in iEEG. Rather, spatial resolution depends on the grouping across individuals and the type of analysis and inference that one aims to make.

Overall, this approach to iEEG and its findings reconcile—at least partly—two main views of the large-scale functional organization of face selectivity in the VOTC: on the one hand, the clustered organization identified by fMRI studies in individual participants[19,21,33,55] (Fig. 1B) and on the other hand, the widely distributed face-selective responses found with iEEG studies[39,46,60] (Fig. 3). Although face-selective populations of neurons are present across the whole VOTC, they are more densely distributed in specific regions such as the right latFG.

A set of three face-selective regions in the anterior VOTC

Critically for the issue raised at the beginning of the review, there is a wide distribution of face-selective responses in the anterior section of the VOTC in specific and reproducible anatomical locations across individual participants: in the antCoS, antOTS, and antFG (Figs. 5B and 6A, for an example of face-selective response in the anterior VOTC in a single participant, see Fig. 8). Such wide distribution in the anterior VOTC goes well beyond what was found previously in fMRI. Because of the susceptibility artifact around the ear canal, fMRI studies reported small and inconsistent face-selective activation in the anterior VOTC and, if it were the case, only in the antCoS, very anteriorly.[22,23,29–33] Moreover, as also mentioned above, few iEEG studies reported face-selective responses in the anterior VOTC. Three key aspects may account for the observation of face-selective responses in the ventral ATL with the FPVS-EEG approach:[78] (1) the recording within cortical sulci in SEEG, in which a substantial proportion of ventral ATL face-selective responses were found (antCoS and antOTS), (2) the particularly high SNR of the technique, and (3) the objective criterion to identify even small neural peaks above noise level in the frequency domain.

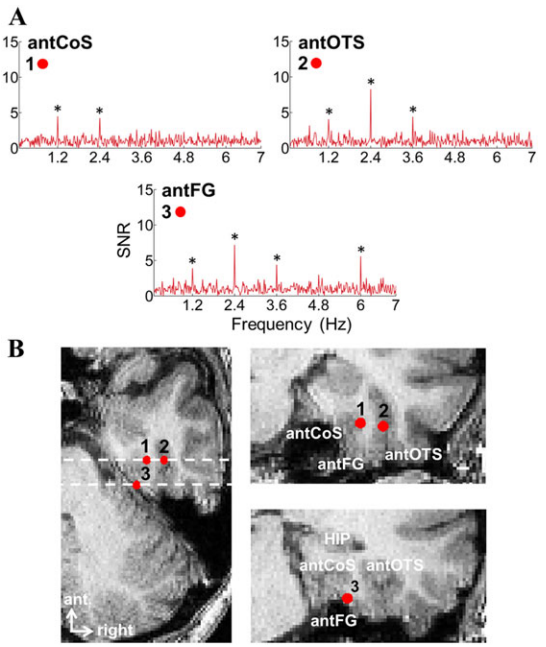

Figure 8. Example of face-selective responses in three distinct anatomical regions of the ventral ATL (from Ref. 78). (A) Face-selective responses recorded from the right antCoS, antOTS, and antFG in a single brain. Note that in the examples shown here for the antCoS and antOTS, no general visual responses were recorded at 6 Hz and harmonics ("face-exclusive" responses). *Statistically significant responses ($Z > 3.1$, $P < 0.001$). (B) Anatomical locations of corresponding recording contacts on MRI slices. Contacts are shown as red dots on axial (left panel) and coronal (right panel) slices. Electrode contacts 1, 2, and 3 are, respectively, located in the antCoS, antOTS, and antFG. The antFG is located between the antCoS and antOTS, at a level where the hippocampus (HIP) is visible on a coronal slice.

A particularly interesting face-selective region is the antFG, located between the antCoS and antOTS,

just anterior to the middle FG (Talairach *y* axis around –30). As illustrated in Figure 1, this region is primarily affected by the fMRI signal dropout and, as a result, has been identified as being face selective only in a handful of fMRI studies.[31–33] SEEG face-selective responses in the right antFG had been previously identified with a conventional approach in a single patient (Fig. 1C), who showed transient prosopagnosia when electrically stimulated in this region.[25] The pattern of responses recorded in the right antFG differs from responses recorded in adjacent regions, such as the right latFG (higher face-selective response) located posteriorly, the antCoS and antOTS (i.e., smaller face-selective response and smaller general visual response at 6 Hz). This suggests that the specific anatomical region of the right antFG is functionally different from adjacent regions (latFG, antCoS, and antOTS). This anatomofunctional specificity of the right antFG has been highlighted thanks to the use of an individual anatomy approach and would have been blurred using a brain normalization approach (Fig. 7A).

Face-exclusive responses at the population level

The careful reader will not have missed two example SEEG spectra in Figure 8 in the antCoS and antOTS showing *exclusive* responses to faces, that is, significant face-selective responses without any 6 Hz general visual response. Such face-exclusive responses are found in increasing proportions from posterior to anterior regions, being maximal in the right ATL,[78] and are also observed in a control experiment with a much lower base rate frequency (1.5 Hz) to rule out a simple low-pass filter effect. Importantly, such EEG spectra have not been found on the human scalp,[75] ruling out an inadequacy of nonface stimuli to evoke population responses as discussed above for the N200/N170.[9,38,39]

Since intracerebral contacts pool the activity of hundreds of thousands of neurons, this finding reveals the presence of exclusive responses to faces at a macroscopic level of cortical organization (i.e., cell population level) for the first time in humans. These responses, which were in highest proportion in the anterior section of the VOTC, may reflect the processing of faces independently from the context (i.e., nonface categories), which could be particularly useful for certain processes that are known to be specific to faces (e.g., encoding and retrieval of information specific to an individual face, holistic processing of individual exemplars, sex, age, expression, social judgments, etc.). An alternative account for these neural responses frequency-locked exclusively to the face stimuli is that they reflect a general response to the only category that is presented periodically in the stimulation sequence, that is, faces in the paradigm[78] (Fig. 4). Indeed, scalp EEG experiments have shown that selective responses to other categories such as houses and limbs inserted periodically in such object sequences can also lead to significant category-selective responses.[43] However, such responses are of much smaller amplitude and are associated with a distinct spatial topography than face-selective responses.[43] Moreover, the face-selective response observed on the scalp is identical whether faces appear periodically or not.[89] Future iEEG studies could build upon such paradigms to assess the exclusivity of the responses to faces particularly in the right VATL (ventral anterior temporal lobe).

Summary and challenges ahead in iEEG mapping of face and visual categorization

Summary and implications for models of face-selectivity

In this review, we presented an approach that overcomes many of the difficulties of iEEG studies to map category-selective responses in the human brain, using faces as a model and recording across the whole VOTC. Thanks to the combination of FPVS, which provides highly sensitive, objective, and quantifiable responses in the frequency domain, with SEEG allowing to record both from gyri and inside sulci of nonnormalized individual brains, we describe a first extensive cartography of face-selectivity in the human VOTC. Besides supporting the wide distribution of face-selective responses across the VOTC, this approach reveals (1) a strong right lateralization of the middle portion of the lateral fusiform gyrus in iEEG; (2) the dominance of this region—corresponding to the so-called FFA in neuroimaging—over all other VOTC regions in relation to the magnitude of the face-selective response; (3) clear face-selective responses in the anterior VOTC, mainly in sulci (antCoS and antOTS); and (4) the presence of exclusive responses to faces in a large proportion of electrode contacts in anterior VOTC regions.

These observations should constrain neurofunctional reviews and models of face processing, which generally fail to incorporate hemispheric specialization, as well as several face-selective/exclusive regions in the VATL[3,5] between the midfusiform gyrus ("FFA") and face-selective clusters in the temporal pole.[4] They also raise novel questions of interest such as whether face-selective or face-exclusive responses functionally differ with respect to sensitivity to other face categorizations (e.g., face identity), and also whether face-selective responses observed outside of the dominant clustered regions are associated with different functional processes.

Importantly, the FPVS-SEEG approach presented here can be used in future studies to measure finer grained face categorization processes, such as individual face discrimination,[90] or the discrimination of various facial expressions,[91] as demonstrated with scalp EEG. Selective responses to other visual categories such as letters and words could also be investigated with the same approach.[92]

Validity of the epileptic brain model, limitations, and the need for large samples

Since iEEG recordings are performed in patients with drug-resistant epilepsy, the validity of this approach to provide a model of the normal functional organization of face-selectivity can be questioned. In this respect, there are a number of methodological issues that need to be considered (e.g., exclude recordings in lesions, artifact rejection if necessary, and selection of patients based on minimal neuropsychological criteria). However, beyond these issues, the neural organization of these patients with long-term drug-resistant epilepsy appears to offer a highly valid model of the typical organization of the human brain. For instance, iEEG and scalp EEG recordings in typical adults show a similar face-selective ERP component in occipito-temporal regions (i.e., N170/N200, iEEG;[37,39,45,47,49] scalp EEG[38,93,94]). Moreover, patients explored with iEEG have so far showed typical fMRI face-selective activations.[17,25,37,43,53] The largest face-selective response in regions identified with fMRI in typical brains (e.g., the right latFG) also provides strong support for the validity of iEEG recordings in the epileptic brain.

One of the limitations of the FPVS-SEEG approach for a large-scale mapping of brain functions is dictated by the sparse-sampling problem, that is, the variable and limited electrode coverage in any given individual participant.[44,88] To deal with such constrain, a large sample of participants is needed to obtain a reliable and global view of the VOTC. For example, while the right IOG is rarely explored in iEEG, this region showed one of the highest face-selective responses in our study,[78] consistent with fMRI observations in typical brains. However, despite a trend for right hemispheric lateralization, there was no significant effect in this region, unlike the clear right lateralization observed in fMRI[33] and the dominant role of the right over the left IOG in causing permanent[95] or transient[37,96–98] individual face recognition impairments. This suggests either a genuine difference between signals collected with different modalities and paradigms or a limitation of the current iEEG approach to capture this lateralization factor in this region. One limitation is undoubtedly related to the large variability between individual patients and recording contacts in terms of response amplitude so that a large sample size is necessary to ensure reproducibility of the findings. In addition, providing that a sufficiently large number of recording contacts across patients are localized in the gray matter of different regions, the *proportion* of significant electrode contacts in a given anatomically defined VOTC region could also serve as complementary information to the average response amplitude.

A large sample of participants also provide the opportunity to refine and fine-tune anatomical subdivisions, as each subdivision will contain a sufficient number of recording contacts to measure reproducible responses. For instance, in the described study,[78] the large sample of participants allowed to split the anterior fusiform gyrus from adjacent sulci. Moreover, thanks to large samples, future iEEG studies might be able to use VOTC cytoarchitectonic divisions that might more closely match functional organization of the cortex than divisions on the basis of macroanatomic landmarks.[60,99,100]

What are the other limitations of the approach? Currently, there is a lack of information about the frequency ranges of stimulation that are associated with the most sensitive and specific responses. The paradigm presented in Figure 4 and used in the described study[78] relies on a 6 Hz stimulation rate, which provides similar responses on the scalp as 12–12.5 Hz rates.[84,89] However, higher

frequency rates may be associated with lower face-selective responses, owing to the limited presentation and duration of (masked) faces. Further validating work is certainly required with scalp EEG to define frequency-tuning functions for various face categorizations.[101]

Timing and high-frequency activity

Besides its high spatial resolution, iEEG also provides a high temporal resolution, which has not been exploited so far in the research program presented here. Several iEEG studies explored the timing of face-selectivity in specific VOTC regions (e.g., the fusiform gyrus[43,48]) but few studies recorded in large samples to understand the temporal dynamics of face-selectivity across the whole VOTC.[39] Future iEEG studies will be needed to understand the timing of face-selectivity in the anterior VOTC. In this respect, even though the quantification and detection of significant responses is performed in the frequency domain to reduce complexity, the FPVS approach can also be used to address questions about the precise timing of neural events. This can be done either by using phase information[102] or by simply averaging epochs of EEG segmented around the events of interest, as performed in the traditional ERP approach but after filtering out the carrier frequency (e.g., 6 Hz[75,76]). With this approach, EEG recorded on the scalp with FPVS leads to complex face-selective responses at multiple time windows between 100 and 600 ms, which are associated with distinct scalp topographies.[75,76,84] Applying the FPVS time-domain analysis to iEEG recordings should help isolating the specific generators of each of these face-selective components recorded on the scalp, and recover precious information to understand the time-course of face categorization processes in the human brain.

Finally, one aspect not addressed yet with FPVS-EEG as presented here is the distinction between low (e.g., ERPs) and high (e.g., HFB) iEEG frequencies.[52,60,69] As explained above, typical iEEG studies in this field tend to concentrate on one or the other, and when both types of activities are analyzed, they have been difficult to reconcile, probably in part due to different analysis parameters[50,60] (but see Ref. 52 for evidence of complementary information to discriminate faces from houses provided by ERPs and HFB). With the approach presented here, the key principle is to frequency-tag the stimulus, that is, project brain activity to a specific frequency, known in advance, and measure a response of interest only at that known frequency. Scalp studies indicate that this approach is very efficient at capturing all of the responses of interest: even if it varies in shape and time, the specific response to faces is periodically locked to the onset of faces, so that all of it is captured in the compact frequency-domain representation. Moreover, response properties of high-frequency activity can also be measured with this approach, by computing the amplitude envelope of the high-frequency signal across time and by performing Fourier analyses.[103] This may offer a potentially powerful approach not only to identify high-frequency activity tagged to the stimuli of interest—here faces inserted among objects—but also to objectively relate or dissociate low- and high-frequency activities related to face categorization or other visual function.

Electrical stimulation to determine critical face-selective regions

iEEG offers the opportunity to electrically stimulate specific face-selective regions in the VOTC, in order to evaluate their causal role in face categorization. Early ECoG studies of Allison and colleagues[9] reported a temporary inability to name photographs of famous faces following electrical stimulation in face-selective (N200) VOTC sites. However, the ability to provide semantic information about the face and the dominance of effects in the left as compared with the right VOTC rather pointed to naming deficits.[104,105] Puce *et al.*[41] described facial hallucinations (isolated eyes, single or multiple faces), without looking at faces, following stimulation of distributed face-selective sites along the posteroanterior axis of the VOTC. More recent ECoG studies have focused on the latFG, reporting facial perceptual distortions in the right but not in the left hemisphere,[59,106] or deficits in face categorization.[107,108]

In SEEG, the spatial coverage of electrodes in the VOTC is more limited in a single patient and the effects of stimulation on face perception have been described less frequently. However, electrical stimulation can be applied directly in the gray matter, allowing for more focal stimulation at lower amplitudes, potentially leading to an increase in specificity of the effect. An early study[109] reported a distortion of faces presented in front of the patient,

following stimulation in the right ventrolateral prefrontal cortex. More recently, Jonas *et al.*[37] reported a case of transient prosopagnosia, that is, a patient who had normal individual face recognition abilities outside of stimulation but suddenly failed to recognize pictures of famous faces following intracerebral stimulation. The site of interest in the right IOG was face selective as determined both with iEEG and fMRI recordings, and the patient was still able to recognize objects during stimulation of the same site. A second SEEG recording in the same area of the same patient led to an impairment in discriminating simultaneously presented pictures of unfamiliar individual faces,[96] ruling out a naming impairment. Electrical stimulation of the right antFG, in the heart of the fMRI susceptibility artifact, also caused prosopagnosia in another patient[25] (Fig. 1C).

In general, iEEG stimulation studies interfering with face perception showed that these effects are confined to face-selective electrodes, and that the amplitude of iEEG responses to faces—which must be related to the density of neuronal populations responding to faces—is positively correlated with the amount of facial perception disturbance[59,108] or face identity disturbance (Ref. 96 with an FPVS approach). Collectively, these observations show that these regions play a critical role in face perception, although it is difficult to relate specific regions to the disturbance of specific face processing subfunctions at this stage. From a practical standpoint, they indicate that iEEG studies should target (i.e., electrically stimulate) regions showing the highest face-selective or face-identity sensitive responses in order to test for their causal role. In this context, and in keeping with the general theme of the review, FPVS-SEEG, with short experiments (i.e., few minutes), straightforward first pass signal analyses (Fourier transform without artifact rejection) and high SNR objective responses also appear advantageous to quickly detect the most important brain regions to target with electrical stimulation.[96]

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Competing interests

The authors declare no competing interests.

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