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Final Report

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Host institution	Université Catholique de Louvain
Supervisor	Prof. Bruno Rossion
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Title of the project	Investigating the temporal dynamics of face processing in the human brain by combining simultaneous measures of scalp and intracranial electrophysiology with functional neuroimaging.

1. Reminder of background and objectives of the proposal

Human faces are ubiquitous within our visual environment and convey a large amount of information crucial for social interactions, such as identity, facial expression of emotion, gender,… Numerous empirical data underline the rapidity with which humans can extract and process this facial information. Brain neuroimaging data indicate that this ability relies on neural computations performed in a network of brain regions in the occipital and temporal visual cortex (Grill-Spector & Weiner, 2014). However, previous research has mostly provided information *either* about the spatial location of regions showing face preferential responses (over other type of stimuli) *or* about the temporal course of face processing at a global level, but not both. Therefore, our understanding of the *temporal* relations between *spatially* distinct face-sensitive regions in the occipito-temporal cortex (i.e. the spatiotemporal dynamics) is currently very limited. On the one hand, in healthy humans the *temporal* dynamics of face processing is usually investigated by recording the electroencephalogram (EEG) on the scalp and the analyses of event-related potentials (ERP) associated with the onset of a face. Overall, ERP studies indicate that multiple face processing stages occur during the time window of the N170 (~120 – 200ms after stimulus onset) , an ERP component recorded bilaterally over posterior temporal scalp regions which is consistently larger in response to images of faces compared to other non-face categories of stimuli (Rossion & Jacques, 2008; Jacques & Rossion, 2006; Jacques et al., 2007). While scalp ERP measurements can provide high temporal resolution information about face perception, they only provide a very coarse estimate of the *spatial* location of cortical regions generating the ERP components involved in face perception (e.g. the N170). Further scalp EEG cannot be used to disentangle the contribution to face perception of distinct but nearby and correlated neural sources.

On the other hand, the *spatial* organization of the face processing network in the human brain has been described using functional magnetic resonance imaging (fMRI) (e.g. Kanwisher et al., 1997; Haxby et al., 2000; Weiner & Grill-Spector, 2010). fMRI research has revealed the existence of a distributed network of cortical areas that show preferential response to faces relative to non-face categories of stimuli (e.g. cars, houses, bodyparts, written words,…) located for the most part in ventral occipito-temporal cortex (VOCT). However, fMRI has two important caveats: First, the low temporal resolution of fMRI measurements (i.e. >1 sec in conventional fMRI) makes it impossible to investigate the temporal dynamics with which these regions are activated or interact. Second, fMRI provides indirect measurements of neural activity and these measurements are prone to local and broad-scale measurements artifacts in the temporal lobe. These artifacts prevent from being able to obtain any signal from large portions of the temporal lobe where potential face-selective regions may be located.

This project aimed at increasing our understanding of the neural basis of face processing by combining different measurements technique allowing focusing both on the spatial and the temporal aspects of face processing. In particular, we were interested in better understanding the neural basis of two fundamental aspects of face processing: 1. which brain regions are involved in *face detection* or *face categorization* (i.e. the detection of a face in the visual environment and the categorization of the face as being a face) and what is their principle of organization?; 2. which brain regions are involved in the coding a face identity and are thus likely involved in face recognition?

2. Methodology in a nutshell

To achieve our goal we relied mostly on recording intracranial electroencephalogram (iEEG) in epileptic patients (at the University Hospital in Nancy, France, with Prof. Louis Maillard). iEEG allows recording electrophysiological neural signals directly from the brain using invasive intracranial electrodes implanted directly on or in the cortex. This procedure is performed for clinical purpose but consent is obtained from the patients to participate in experiments during their stay at the hospital (typically for ~1 week). iEEG is extremely precious as it is the only neuroimaging technique that currently allows measuring

neural signals directly from inside the human brain. Arrays of electrodes composed of contiguous recording contacts (length = 1.5mm spaced 2mm apart) are implanted in the patient's brain (Figure 1). Each recording contact measures electrical potentials (i.e. local field potentials) generated by local neuronal populations (i.e. providing a high spatial resolution of ~2-5mm) with a high temporal resolution (in the order of a millisecond), thereby enabling to jointly investigate both the spatial and temporal aspects of face visual processing. A typical patient has more than 100 recording contacts. Importantly for our purpose, in each patient, each recording contact relevant for our goal (i.e. located in VOTC and showing significant neural response to images of faces) is labelled according to its precise anatomical location in the cortex.

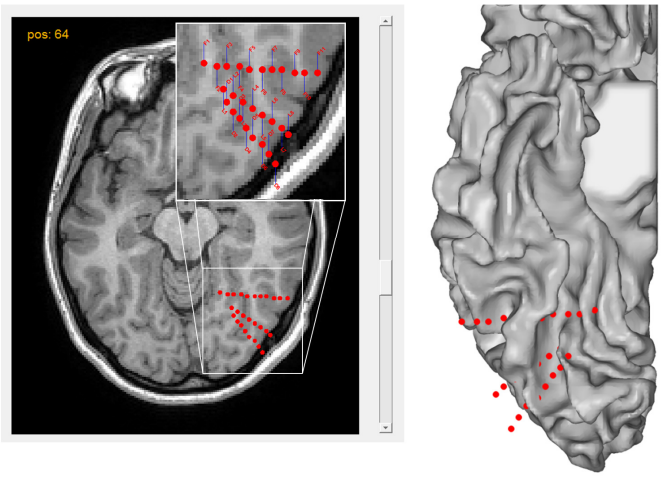

Figure 1: example of three iEEG recording electrode arrays (and corresponding recording contacts in red) in the posterior occipital and temporal lobes (inferior occipital gyrus, fusiform gyrus, occipito-temporal sulcus, inferior temporal gyrus) viewed on an axial MRI slice (left) and in the 3D reconstructed white matter surface of the right hemisphere.

In addition to iEEG, in most patients scalp EEG electrodes were placed to monitor EEG signal at a global level (i.e. the whole scalp). Therefore iEEG and scalp EEG were measured simultaneously which may help bridging findings about face processing made using either recording technique and help better understand the neural origin of the scalp-recorded electrophysiological activity related to face processing. When possible and interesting, we also collected fMRI data from the same patients to link face-related iEEG and scalp EEG signals to fMRI-defined face-selective responses in VOTC.

In the original research project we restricted our research questions mostly to the investigation of the neural sources of the N170 ERP component (i.e. N170 face selectivity and sensitivity to face identity) using traditional transient event-related potential (ERP) stimulation technique (i.e. presenting one stimulus at a time in a relatively slow stimulation sequence). We brought several modifications to the proposed experimental questions and research design for the following reasons: 1) We wanted to be able to tackle broader scientific questions related to face processing and to more easily disentangle the contribution of genuine face-selective responses from 'general visual responses' (i.e. responses which are not related to the 'faceness' of the stimulus) in the recorded electrophysiological signal; 2) we needed to accommodate with the requirements of the clinical setting in which the data is collected (i.e. need for short experiments) and yet collect reliable high signal-to-noise ratio data. **To achieve this we used an original stimulus presentation approach called '*Fast Periodic Visual Stimulation*' (FPVS) (Rossion & Boremanse, 2011)** which is based on the 'steady state visual evoked potential' (SSVEP) approach developed originally by Regan (Regan, 1966). The FPVS paradigm relies on the finding that presenting a train of stimuli (e.g. visual) at a determined periodic rate/frequency generates a periodic electrophysiological response at the same frequency as the stimulation frequency. In this framework, electrophysiological data are analysed either through classical frequency analyses (i.e. Fourier transform) in which response to the stimulation is objectively quantified by measuring the response amplitude at the specific stimulation frequency, or by more sophisticated time-

frequency analyses (e.g. wavelet or Hilbert transform) which allow quantifying the modulation of signal amplitude at the stimulation frequency as a function of time.

3. Results

3.1. Investigating the organization of face-selectivity in the ventral occipito-temporal cortex using fast periodic visual stimulation (related to part 1 of the research project).

3.1.1. Objectives

Our main goal in this study was to provide a comprehensive characterization of face-selective responses (i.e. anatomical location and magnitude of face-selectivity) in VOTC using intracranial recordings, and to relate these signals to electrophysiological activities measured on the scalp. While fMRI studies have provided detailed information about the spatial organization of face-selectivity in VOTC, the measurement of fMRI signal suffers from both local- and broad-scale measurements artifacts mostly in the anterior half of the temporal lobe (i.e. susceptibility artifact). Therefore, because some regions of the temporal lobe have very low signal-to-noise ratio in fMRI, this technique cannot provide a fair comparison of face-selectivity across different VOTC regions. Because intracranial recordings measure local electrophysiological activity, they do not suffer from such measurements artifacts. We therefore used this methodology to map face-selectivity across multiple regions of the VOCT. This study directly relates to the first set of experiments of the original research proposal as it aims at identifying the network of face-selective regions in VOTC and determine its organization.

3.1.2. Methods, results, discussion

Here we used a modified version of the FPVS approach (see section 2. 'methods') to isolate face-specific responses. In this version (called 'oddball FPVS', Rossion et al., 2015; Jacques et al., in preparation, see Figure 2A), the subject is presented with sequences of images appearing at a rate of 6 Hz. Each FPVS sequence lasts for 70 seconds (Figure 2B). In each sequence, most of the images presented are natural images of non-face categories (living and non-living, natural and man-made categories). However, during the sequence, every fifth stimulus presented is an image containing a human face; and face images do not appear at any other time during the sequence. Thus, in the sequence faces are presented at the precise rate of 1.2Hz (1 face every 5 images presented at 6Hz). The stimulation sequence is thus composed of 2 distinct frequencies, 6Hz and 1.2HZ, corresponding respectively to the presentation frequency of various non-face categories and to the presentation frequency of various face images (Figure 2A). Using this oddball FPVS approach therefore allows to objectively isolate the response to images of faces from the response to images of non-faces presented within the same stimulation sequence (because these responses appear in distinct frequency bands of the iEEG response). As control conditions, we also recorded signal for sequences where face images were replaced by either images of houses or bodyparts (upper and lower limbs). Importantly, the FPVS approach allows to obtain responses with a high signal-to-noise ratio in a short amount of time. Indeed, each patient was presented with 2 to 4 sequences of the face condition.

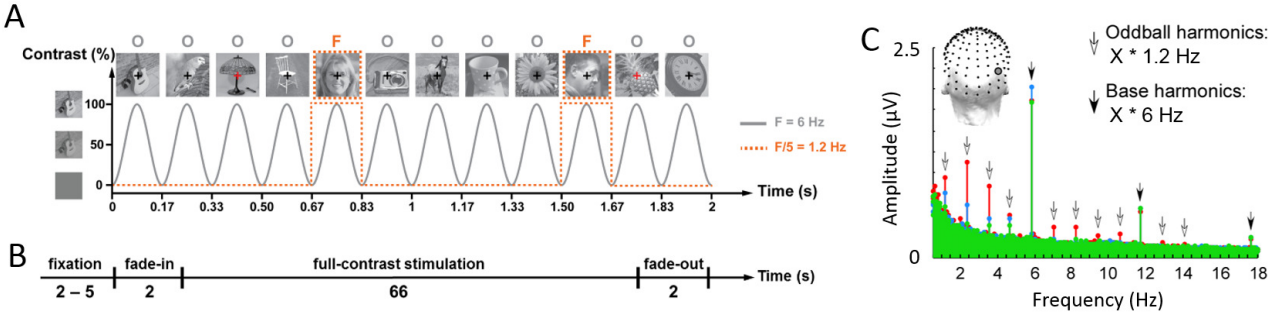

Figure 2: A. The fast periodic visual stimulation paradigm. Images of objects were presented by sinusoidal contrast modulation at a rate of 6 stimuli per second (6 Hz). A different face image was presented every 5 stimuli (i.e., appearing at the frequency of 6 Hz/5=1.2 Hz). B. Timeline of a whole visual stimulation sequence. A sequence started by a fixation cross displayed on a gray background for 2 to 5s (random duration) in order to stabilise subjects' fixation, followed by a 70 s sequence of image presentation which started by a 2s face-in period and ended with a 2s fade-out period (66s of full-contrast stimulation). C. Frequency domain representation of the scalp EEG signal at one occipito-temporal electrode for faces (red), bodyparts (blue) and houses (green). Electrode location is shown on the 3D head plot viewed from the back of the head. This shows both category-selective responses at oddball frequencies (~1.2 Hz and harmonics) and general visual responses occurring at ~6 Hz and harmonics.

We first validated the oddball FPVS experimental design with face and non-face (houses and bodyparts) stimuli by running a **scalp EEG experiment** in healthy young adults in the laboratory (see attached manuscripts: '*The spatio-temporal dynamics of category-selective responses to natural images as evidenced with fast periodic visual stimulation'* and '*Fast periodic presentation of natural images reveals a robust face-selective electrophysiological response in the human brain'*). This experiment confirmed that we can isolate 2 distinct responses which correspond respectively to a general visual response to all categories (at 6Hz and harmonics: 12, 18Hz,…) as well as an oddball category-selective response (at 1.2Hz oddball frequency and harmonics: 2.4, 3.6, 4.8Hz,…) (Figure 2C). This oddball response was largest for faces and had the typical scalp distribution of face-selective responses as measured in traditional ERP/N170 experiments. Moreover, the distribution of responses on the scalp for face, house and bodypart images were significantly different and corresponded with the known anatomical location of category-selective responses in the VOTC measured with fMRI. We also were able to analyse this data set using traditional time-domain (in contrast to frequency domain) analyses to have access to the temporal dynamics of face responses on the scalp. This showed that the oddball response was composed of an N170-like response (similar to that observed in traditional transient ERP experiments, Rossion & Jacques, 2008), as well as a several novel face-selective response occurring both slightly earlier and later than the N170 and with a scalp distribution suggesting a source in the posterior inferior occipital cortex and another source in the ventral part of the middle temporal lobe. This is an exciting result as it shows that FPVS can not only be used to measure reliable responses in a short amount of time, but also provides access to additional information concerning the processing of visual stimuli such as faces.

Intracerebral electrophysiological data from this oddball FPVS face-selectivity 'localizer' was obtained in 20 epileptic patients who had at least 1 recording site in the occipital or the temporal lobe (representing ~1600 recording sites). A first type of analysis allowed characterizing the magnitude and quality of face-selectivity along the ventral occipito-temporal cortex (VOTC) by quantifying separately the face/oddball response (occurring at 1.2Hz and harmonics) and the general visual response (occurring at 6Hz and harmonics). To achieve this we first isolated all VOTC electrodes in all patients that had significant oddball/face response (308 electrodes) and labelled each recording contact as a function of its precise anatomical location in 6 anatomical regions of the VOTC (Figure 3A) which roughly correspond to anatomical locations where face activations have been described with fMRI. Next, we quantified for each electrode the amplitude of response to faces/oddball, the amplitude of the general visual response (Figure 3B) and the ratio between the two which provides a way to estimate the degree to which the response from the cortical tissue around the electrode is driven more by face stimuli or by non-specific stimuli (non-face images of various categories).

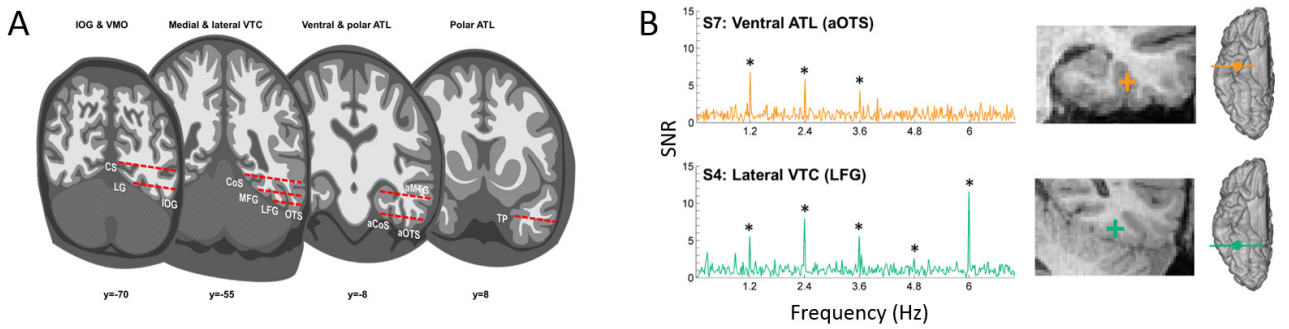

Figure 3: A. Schematic representation of the typical location of iEEG recording electrodes in VOTC where face-selective regions are found. The panel shows four schematic coronal slices with electrodes and recording contacts displayed in red. B. Typical face-selective and general visual responses recorded in two regions of the VOTC. Left panel displays typical frequency domain representations of the iEEG recorded in two different VOTC regions (taken from single recording contacts). Face-selective responses occur at oddball frequencies (1.2, 2.4, 3.6 and 4.8 Hz). General visual responses occur at the 6 Hz base frequency. Top row shows a face-exclusive response in ventral anterior temporal lobe where the general visual response is completely absent. Right panel shows the anatomical locations of the corresponding recording contacts (on a coronal MRI slice and schematically over a reconstructed cortical surface using the Colin27 brain). * Indicates statistically significant responses (Z>3.1, p<0.001).

We reported four main findings (see attached manuscript: *A gradual increase of face-selectivity in the human ventral occipito-temporal cortex*): First, we report a widely distributed network of regions responding selectively to images of faces throughout the VOTC, with face-selective responses being observed from posterior to anterior VOTC (ventro-medial occipital, inferior occipital gyrus, lateral and medial ventral temporal cortex, anterior collateral and occipito-temporal sulci, temporal pole and anterior middle temporal gyrus). Interestingly, we found three distinct regions within the anterior ventral temporal lobe (anterior collateral sulcus, anterior occipito-temporal sulcus and temporal pole). This is most interesting because this cortical territory is affected by strong measurements artifacts in fMRI, and reliable measurements of face-selectivity in these regions are difficult to obtain. Therefore our iEEG measurements allowed to identify previously unknown face-selective responses within the VOTC. Second, we observed different patterns of responses across this VOTC network for general visual responses and face responses. While the magnitude of the general visual response decreases monotonically from early visual cortex in the posterior occipital regions to the anterior temporal lobe, face response increases from posterior regions to the lateral fusiform gyrus (middle temporal lobe) and then slightly decreases in more anterior regions. Third, computing the ratio between face and general visual responses reveals for the first time a gradual increase in face preferential (i.e. oddball/visual) responses from posterior to anterior face-sensitive regions of the VOTC. Fourth, in the most anterior regions we found a large proportion of recording sites showing *face-exclusive* responses (Figure 3B, top), that is, significant responses at the face/oddball frequency with an absence of response at the base stimulation frequency (general visual response).

These findings confirm and refine the widely distributed network for face processing in VOTC, with 3 distinct face-selective regions in the anterior temporal lobe. Within this network, we found an increase of face-selectivity along a posterior-anterior axis of VOTC, suggesting face-selectivity is an organizing principle of the face perception network. This is in line with the hierarchical view of visual processing and the general spatial organization of visual functions in VOTC. In addition, we found face-exclusive responses in ATL regions, indicating for the first time that strict face-specificity can be found at the macroscopic scale of local populations of neurons (whereas it was only previously only described at the level of single neurons). These face-exclusive representations may reflect high-level and context-independent face processing associated with encoding and retrieval of information specific to individual faces (which is supported by specific connections between ATL regions and the medial temporal lobe).

3.1.3. Future directions for data analyses

This data set is extremely rich and can be analysed in numerous ways to extract different type of information about face categorization/detection in the VOTC. A *first* ongoing analysis is the computation of the stimulus driven periodic modulation of the power in higher frequency bands of the electrophysiological signal (i.e. gamma or broadband frequencies) using time-frequency analyses (wavelet analyses). These high frequency broadband signals are thought to reflect firing rate of neurons at a neuronal population level and may therefore provide complementary information about the neural processes involved in categorizing faces, compared to lower frequency signals (i.e. which have been the focus of our previous analysis). As a *second* additional step in the analyses, the phase information associated with the face/oddball fundamental frequency (1.2Hz) can be extracted. The phase can be used to index the latency at which a response is measured at a given recording contact and should allow estimating the relative timing of activation in the different face-selective VOTC regions highlighted, as well as the dynamic coupling between distant brain regions (i.e. phase coherence analyses). *Third*, so far this data was mostly characterized by measuring amplitude in the frequency domain, which does not provide temporal information. However, this data is currently also being analysed in the time domain to recover further temporal information and examine different subcomponents of the face response arising at different latencies. *Fourth*, given the high signal-to-noise ratio of the SSVEP technique, this study will allow to investigate the relationship between face electrophysiological signals measured intracranially and at scalp level to better understand the neural origin of scalp-measured EEG signals.

Aside from the FPVS oddball 'face-localizer' experiment we also run a **standard ERP experiment in iEEG** with the exact same images as those used in the FPVS experiment. This experiment also directly relates to the first study of the original research project. Here, each image is flashed for 0.3 sec with a random delay of about 1.6 sec separating each image. Here we showed images of faces, houses, bodyparts and inverted faces. The goal of this experiment was two-fold: (1) validate the findings about face-selectivity from the FPVS experiment and anchor these findings in the existing iEEG literature which mostly used ERP experimental designs; (2) explore the sources of the scalp-recorded N170 and its positive dipolar counterpart on the vertex (i.e. top of the head). The analysis and result description for this study is ongoing.

3.2. Investigating spatial and temporal dynamics of face identity coding in VOTC (related to the second set of studies of the original research project).

3.2.1. Objectives

Humans are extremely fast and effective at recognizing or discriminating individual faces despite large changes of appearance between different images of the same individual. Using scalp EEG we have shown previously that the encoding of an individual face representation takes place rapidly, between 150 and 200ms after stimulus onset, in the time-window of the scalp N170 ERP component (Jacques & Rossion, 2006; 2009; Jacques et al., 2007). Here we used iEEG to investigate the contribution and temporal dynamics of different face-selective regions of the VOTC to the encoding of an individual face representation.

3.2.2. Methods and results

As for the first main study of the project (section 3.1) we adapted the original experimental design to investigate the coding of face identity using the FPVS oddball approach during iEEG recording. Briefly, in each 60 seconds stimulation sequence a base face (e.g. face 'A') is presented at a rate of 6Hz and in every 5th image presentation (i.e. at 1.2Hz), a different face identity is presented instead of face A (e.g. AAAABAAAACAAAAD…). The magnitude of the oddball response (i.e. at 1.2Hz and harmonics) provides an estimation for how well the neurons in the cortex surrounding the recording site can discriminate between distinct facial identities. The patients were presented with two types of sequences: either all faces were in the upright orientation or in the upside-down orientation. This was done to be able to isolate genuine face identity discrimination oddball responses from responses simply related to the periodic change of image (i.e.

the lower-level visual properties associated with this change of image). Brain regions that show larger oddball responses for upright compared to upside-down faces are associated with facial identity discrimination. As for the first FPVS experiment, this data is being analysed both in the frequency (amplitude and phase) and time domains.

We collected data on this experiment for 35 patients, of which 25 showed significant oddball identity discrimination responses in VOTC either with upright or upside-down faces. Again, recording contacts showing significant discrimination responses (284 contacts in 25 patients) were grouped by anatomical location according to their antero-posterior and latero-medial position in VOTC. The frequency domain analyses reveal two very interesting findings: *first*, only three VOTC regions showed overall larger responses for upright compared to upside-down faces (indicating genuine face identity discrimination), which were all located along the fusiform gyrus (posterior fusiform gyrus, lateral/middle fusiform gyrus, anterior fusiform gyrus) (Figure 4). Surprisingly, other face-selective regions (which were isolated in study 3.1) in more anterior part of the temporal lobe did not exhibit stronger response for upright compared to upside-down face discrimination. Second, although there was roughly an equal number of recording contacts in the right and left hemispheres, there is a very striking dominance of the right hemisphere for face discrimination responses where the vast majority of the recording contacts showing significant facial identity discrimination responses (and the largest in amplitude) were located in the right hemisphere. Again, this was not the case for the first FPVS experiment which reflect face detection/categorization. This brings strong and direct support to the right hemispheric dominance of face identity processing in humans identified in brain lesioned patients suffering from face recognition deficits (prosopagnosia).

Data for this experiment are currently still being analysed. While the first pass of analyses has already allowed identifying highly promising and novel findings, further analyses of the data in the time-domain will provide additional information about the temporal dynamics of activations of these distinct regions coding for face identity.

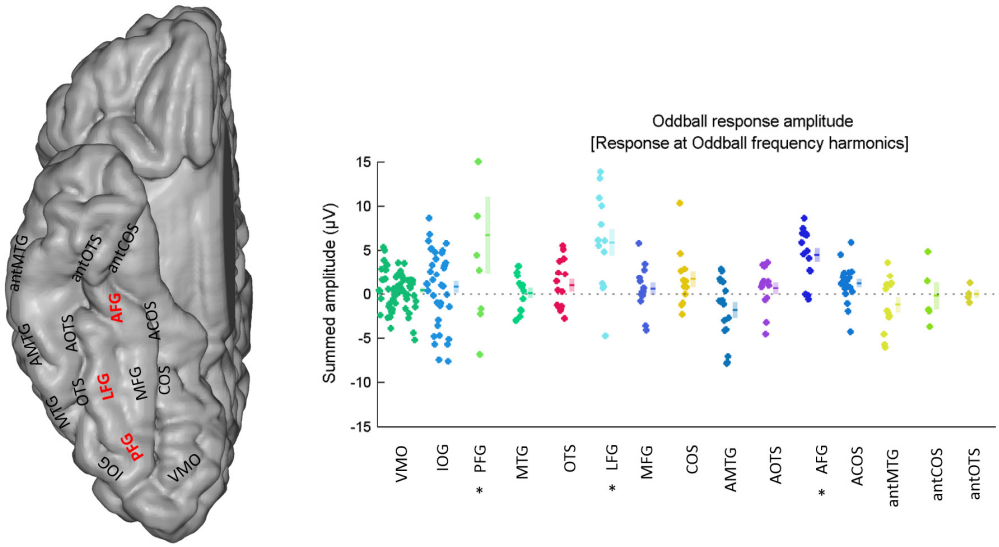

Figure 4: Magnitude of the face inversion effect across multiple VOTC regions. The figure represents the difference between the amplitude of the face discrimination 'oddball' response measured in the upright face sequences vs. inverted face sequences. Each dot represents a recording contact, which were pooled across 35 participants and grouped by anatomical brain regions and averaged across hemispheres (see each region location on the ventral view of the temporal lobe on the left). Three regions along the fusiform gyrus (PFG: posterior fusiform gyrus; LFG: lateral fusiform gyrus; AFG: anterior fusiform gyrus) show significantly larger identity discrimination responses in the upright face condition. When splitting the data by hemisphere, there was a striking dominance of the right hemisphere which contained most of the significant face identity discrimination responses.

In this first experiment on face identity coding it was surprising not to find face identity discrimination responses in anterior temporal regions. Because it is thought that the anterior part of the

temporal lobe is particularly involved in coding and retrieving representations of familiar faces (the anterior temporal lobe is heavily connected with brain structures involved in memory in the medial temporal lobe) we postulated that the lack of face identity discrimination responses in these regions might be related to the fact that we used images of faces that were unfamiliar to the patients. It might be that these regions would have generated identity discrimination responses had we used familiar faces instead of unfamiliar ones. In order to test this hypothesis, we conducted an additional experiment where we used unfamiliar as well as familiar/learned faces. Patients had to first thoroughly learn a set of previously unfamiliar faces (using a large number of different images of the same individual and a relatively long training protocol). In this experiment, FPVS sequences were either upright or upside-down faces which either familiar/learned faces or completely unfamiliar faces. Patients were tested with this set of faces both before and after training to be able to attribute any change in the responses to the familiarization training itself. Because this experiment required relatively long training and testing protocols, we first piloted this experiment on a set of healthy young adults using scalp EEG recordings in the laboratory. This was done using the same training and testing protocol, except these were extended in time to make sure we could measure effects of familiarization. Both the scalp EEG and iEEG data (still being collected) are being currently analysed.

3.3. Linking functional cortical activity across intracranial and scalp recording of electrophysiological signal.

3.3.1. Objectives

As part of the original research project we also aimed to investigate the relationship between electrophysiological responses measured on the scalp and inside the brain using iEEG. A better understanding of such a relationship would allow to provide a better estimate of the neural origin of the different face-related EEG responses measured on the scalp.

3.3.2. Methods and results

Our first attempt at relating scalp EEG and iEEG was performed in a single patient. This patient is used as a test bed for our approach because 1) she had a limited number of intracranial recording contacts (i.e. 28) that were in contact with two different face-selective regions in the inferior occipital gyrus and fusiform gyrus (therefore offering both an opportunity to observe separate contributions of these 2 regions to the scalp EEG signal and yet a limited data set to deal with); 2) she had a very clean EEG scalp recording with 32 channels spread over the whole scalp (Figure 5A. The patient completed a number of experiments including FPVS face studies and traditional transient ERP studies. In a first experiment we found that the intracranial contacts that showed the strongest response to facial identity (i.e. face adaptation) were closest to the scalp electrodes also showing the strongest response to facial identity (Figure 5A). To further quantify this relationship we correlated the modulation of amplitude at the visual stimulation frequency (6 Hz) as a function of time across scalp and intracranial electrodes. This showed that the visual response measured at intracranial electrodes located in two different face-selective regions in VOTC correlated with a slightly different set of scalp electrodes (Figure 5B). This is highly interesting and promising because it shows that even with a limited number of scalp electrodes (32 electrodes here) we can dissociate the activity from two nearby face-selective regions in VOTC. This will prove extremely useful when interpreting data collected from scalp EEG alone, which is currently the only way to collect electrophysiological data in healthy human individuals. We also reveal dissociations in the phase of the signal across adjacent intracerebral recording contacts which can help resolve the precise location of the face-selective regions in cortex. Data from this experiment is currently under analyses and will be used as an opportunity to develop tools to investigate the relationship between scalp EEG and iEEG, as well as a proof of concept for our methodology.

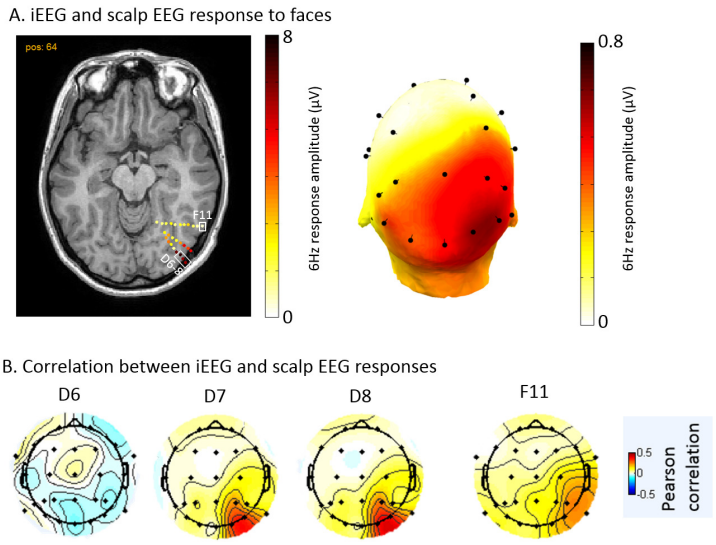

Figure 5: Correlation between EEG recorded on the scalp simultaneously with iEEG in a single patient. A. Spatial distribution and amplitude of response to faces at 6Hz in a FPVS paradigm in iEEG (left, axial slice) and scalp EEG (right, tilted view from above and back of the head). On the left, intracerebral recording contacts are colour-coded as a function of the response amplitude. On the right, the scalp map shows the distribution of response to faces across the back of the head. B. Pearson correlations between the signals measured at four different iEEG recording contacts (D6-D8, F11; location shown in A) and scalp EEG at each scalp electrode (shown as scalp maps viewed from above the head, nose on top). This shows strong correlation between some iEEG contacts located close to the scalp, but not all (e.g. contact D6 is not correlated with signal on the scalp). In addition, the pattern of scalp correlation is different for contacts located in the posterior inferior occipital gyrus (D6-8) and more anterior contact located in the lateral inferior temporal gyrus (F11).

3.4. Involvement in other related projects.

During the course of this research project we also participated in a number of studies carried out in our lab in collaboration with the CHU in Nancy and directly related to the current research project.

First, we were involved in testing an epileptic patient before (in iEEG and fMRI) and after (in fMRI) a surgery to remove a small part of the brain tissue responsible for generating the epileptic seizures. What was unique about this patient is that the cortical tissue targeted to be removed contained one of the face-selective region in inferior occipital gyrus, identified both with fMRI and iEEG recordings before surgery. Surprisingly, the activations and organization of the face-processing network was remarkably similar before and after surgery, despite removing an important node of the face processing network in visual cortex. This reveals the remarkable resiliency and plasticity of the face processing system after a limited brain lesion. See attached manuscript: '*High-level visual networks are resilient to focal cortical resection in the human brain.'*

Second, we were involved in the analyses of iEEG and fMRI data from epileptic patients in which clinical-oriented electrical stimulation of face-selective regions (as identified as face-selective both by fMRI and iEEG data) generate deficits or perturbation of face perception. These studies are crucial because they allow to establish a direct causal role of a given face-selective region in face perception. These studies therefore supplement correlational studies (i.e. a particular region is activated by a stimulus) which cannot prove the necessary contribution of the region in the function. See attached manuscripts: *1. Intracerebral electrical stimulation of a face-selective area in the right inferior occipital cortex impairs individual face discrimination.* ; 2. *Beyond the core face-processing network: intracerebral stimulation of a face-selective area in the right anterior fusiform gyrus elicits transient prosopagnosia.*

3.5. Bibliography

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4. Scientific Diffusion

4.1. Manuscripts published, submitted or in preparation, in relation with the mandate

Jacques, C., Retter, T., Rossion, B. The spatio-temporal dynamics of category-selective responses to natural images as evidenced with fast periodic visual stimulation. *in preparation*. (attached to the final report).

Jacques, C., Jonas, J. , Maillard, L., Rossion, B. The intracerebral face-selective P170 in the ventral occipito-temporal gyri and sulci. *in preparation*.

Jonas*, J., Jacques*, C., Brissart, H., Colnat-Coulbois, S., Maillard, L., Rossion, B. A gradual increase of face-selectivity along the human ventral visual pathway: direct evidence from intracerebral recordings with fast periodic visual stimulation, *submitted*. *Equal contribution. (attached to the final report).

Rossion, B., Torfs, K., Jacques, C., Liu-Shuang, J. (2015) Fast periodic presentation of natural images reveals a robust face-selective electrophysiological response in the human brain. *Journal of Vision*, 15, 18. doi:10.1167/15.1.18. (attached to the final report).

Jonas, J. Rossion B., Brissart, H., Frismand, S., Jacques, C., Hossu, G., Colnat-Coulbois S., Vespignani H., Vignal J-P, Maillard L. (In Press) Beyond the core face-processing network: intracerebral stimulation of a face-selective area in the right anterior fusiform gyrus elicits transient prosopagnosia. *Cortex*.

Jonas, J., Rossion, B., Krieg, J., Koessler, L., Colnat-Coulbois, S., Vespignani, H., Jacques, C., Vignal, J.-P., Brissart, H., Maillard, L. (2014). Intracerebral electrical stimulation of a face-selective area in the right inferior occipital cortex impairs individual face discrimination. *NeuroImage*, 99, 487-497. (attached to the final report).

Weiner, K.S., Maillard, L., Jonas, J., Brissart, H., Hossu, G., Jacques, C., Loftus, D., Gomez, J., Grill- Spector, K., Rossion, B. High-level visual networks are resilient to focal cortical resection in the human brain. *submitted*. (attached to the final report).

4.2. Manuscripts published outside the frame of the mandate (with a reference to BELSPO as the funding source)

Rangarajan, V., Hermes, D. Foster, B. L. Weiner, K.S. Jacques, C., Grill-Spector, K. Parvizi, J. (in press). Electrical Stimulation of the Left and Right Human Fusiform Gyrus Causes Different Effects in Conscious Face Perception. Journal of Neuroscience. (attached to the final report).

Jacques, C., Schiltz, C., Goffaux, V. (2014). Face perception is tuned to horizontal orientation in the N170 time window. Journal of Vision, 14(2):5, 1–18, http://www.journalofvision.org/content/14/2/5, doi:10.1167/14.2.5. (attached to the final report).

Jacques, C., Witthoft, N., Weiner K.S. , Foster, B.L. , Rangarajan, V., Hermes, D., Miller, K. Parvizi, J., Grill-Spector, K. Corresponding ECoG and fMRI category-selective signals in human ventral temporal cortex.. In revision. (attached to the final report).

4.3. Presentations at international conferences/workshop

The present work was presented at several international conferences. The conferences are high level international conference which allow sharing the findings with a very wide audience of scientists in Vision Science and Neuroscience. We also presented our work at a smaller workshop organized in Israel and invited by Prof. Galit Yovel (Tel Aviv University) and gather a group of senior internationally reknown experts in the field of face visual processing.

Jacques, C., Retter, T., Rossion, B. The spatio-temporal signatures of category-selective responses to natural images as evidenced with fast periodic visual stimulation. Vision Science Society meeting 2015.

Weiner, K.S., Maillard, L., Jonas, J., Hossu, G., Brissart, H., Jacques, C., Loftus, D., Grill- Spector, K., Rossion, B., The human face processing network is resilient after resection of specialized cortical inputs. Vision Science Society meeting 2015.

Rossion, B. Jonas, J., Jacques, C., Liu-Shang J., Maillard, L. A gradual increase of face-selectivity along the human ventral visual pathway: evidence from intracerebral recordings with fast periodic visual stimulation. Vision Science Society meeting 2015.

Jacques C., Jonas J., Liu-Shang J., Maillard L., Rossion B. A gradual increase of face-selectivity along the human ventral visual pathway: direct evidence from intracerebral recordings with fast periodic visual stimulation. Worshop: 'On Faces, Bodies and Voices: Multimodal Mechanism of Person Recognition', Israel: 16-19 mars 2015.

Jonas J., Jacques C., Liu-Shang J., Maillard L., Rossion B. A gradual increase of face-selectivity along the human ventral visual pathway: direct evidence from intracerebral recordings with fast periodic visual stimulation. Society for Neuroscience meeting 2014.

Weiner, K.S., Maillard, L., Jonas, J., Hossu, G., Brissart, H., Jacques, C., Loftus, D., Grill- Spector, K., Rossion, B., The resiliency of cortical networks: Stable functional organization of the face processing network after surgical resection of the right inferior occipital gyrus. Society for Neuroscience meeting 2014.

Weiner, K.S., Maillard, L., Jonas, J., Hossu, G., Brissart, H., Jacques, C., Loftus, D., Grill- Spector, K., Rossion, B., Removing the right inferior occipital gyrus does not disrupt face-selective responses in human ventral temporal cortex: Evidence against a strict hierarchical model of face perception. Vision Science Society meeting 2014.

Jonas, J., Rossion, B., Krieg, J., Koessler, L., Colnat-Coulbois, S., Vignal, J.-P., Descoins, M., Jacques, C., Vespignani, H., Maillard, L. Neural Coding of Individual Faces in the Human Right Inferior Occipital Cortex: Direct Evidence from Intracerebral Recordings and Stimulations. Vision Science Society meeting 2013.

Jacques, C., Witthoft, N., Weiner K.S. , Foster, B.L. , Rangarajan, V., Hermes, D., Miller, K. Parvizi, J., Grill-Spector, K. Electrocorticography of category-selectivity in human ventral temporal cortex: spatial organization, responses to single images, and coupling with fMRI. Vision Science Society meeting 2013.

Jonas, J., Maillard, L., Colnat-Coulbois, S., Vignal, J.-P., Jacques, C., Rossion, B. Neural Coding of Individual Faces in the Human Right Inferior Occipital Cortex: Direct Evidence from Intracerebral Recordings and Stimulations. Society for Neuroscience meeting 2013.

5. Conclusions: scientific and technical implications, pitfalls, carrier perspectives

Overall this research project was a success and the main *scientific* objectives of the two sections of the research agenda have been reached. First, by recording a first large dataset we were able to characterize important properties of the spatial organization of multiple face-selective regions in VOTC which participate in face categorization (study 1, section 3.1). Current analyses of the same data will provide further information about the temporal aspects of face detection/categorization. Second, recording a second large data set, we identified face-selective VOTC regions involved in facial identity processing (study 2, section 3.2). Again, time-domain analyses of the same data will allow to determine the temporal dynamics of face identity coding in VOTC. These findings represent fundamental contributions for the scientific community. These contribution are particularly important because they were achieved using a very large sample of participants (up to 35 patients) with a unique methodology which gives access to direct local measurements of neural activity within the living human brain. Very few laboratories in the world have access to this type of data, and even fewer are able to test as many patients as what we have here. There is no doubt that this

research will have a strong impact on the field of visual neuroscience and will be acknowledged by a large number of researchers in the field.

From a *technical* point of view, this research project has also allowed to develop a series of tools and analyses pipelines to collect, visualize and analyse the iEEG data in relation to the particular brain structure in which the signal is recorded. Moreover, the use of an original FPVS experimental approach to study high-level face perception is both novel and very promising. Indeed, we showed it could be used to map various face perception functions highly effectively and in a short amount of time. This project thus allowed paving the road to use the FPVS approach in other research domains with iEEG recordings. The tools and expertise developed in the lab during the course of the research project will be used in future project in the lab and may potentially be disseminated to other labs in the future.

In the original research project, we had planned to scan most patients in fMRI to identify face-selective regions from which we would record iEEG responses. The goal was to investigate the processing dynamics (as recorded in iEEG) between several face-selective regions identified with fMRI *in the same patient*. This particular point of the original project was more problematic than expected and we tested a few patients in fMRI, mainly for purpose of locating (relative to fMRI-defined face-selective regions) intracranial electrode generating face perception deficits with electrical stimulation, or locate a particularly interesting contact in one of our experiment. The reason we did not scan most of the patients was due to the fact that it was more challenging than expected to collect data from patients that had simultaneous electrodes in multiple face regions within VOTC. This is because the electrode implantation is highly unpredictable and variable from patient to patient (driven by clinical practice), and most patients had electrodes in a single (occasionally two) face-selective region at a time. The fact that we could rarely measure responses from several face-selective regions in the same individual patient made it less interesting to collect fMRI data in each individual patients. Looking at the data we have collected so far, we feel the lack of fMRI data is not that problematic. Indeed, the face-selective responses identified in iEEG are very well localized and anatomically reproducible across patients, so that we could most of the time unambiguously identify and label in each patient the region which corresponds to known fMRI-defined face-selective regions in human adults. To solve the issue of not being able to collect data simultaneously from several face-selective regions in individual patients we relied on a group approach (i.e. grouping data from a large sample of subject) to characterize the face perception system in ventral occipito-temporal cortex. This turned out to be a very satisfactory solution. Moreover, we discovered that we could find several additional face-selective regions in iEEG that cannot be measured with fMRI due to measurements artifact.

During the course of this research project I was able to bring my expertise in signal processing, electrophysiology and programming skills to the lab where the research was performed. This clearly helped going further in terms of data exploration, analyses and visualization. This research project was performed in a wider research program involving a collaboration between the Université Catholique de Louvain (prof. Bruno Rossion) and the Université de Lorraine / CHU-Nancy in France (prof. Louis Maillard). This type of collaboration is fundamental to increase the visibility of the local laboratory as well as the UCL as a whole. Further, it not only helps promoting research done in Belgium, but also increases the chances of obtaining large national, international or European research grants. The data collection and processing, as well as the development of analyses and visualization tools is typically very long in this type of project (a lot of the tools had to be built from scratch). This explains why the main studies in these projects have not yet been published, although we have participated in the elaboration and publication of several studies directly related to this research project. Again, given the nature of the data and findings there is no doubt that current and future manuscript based on the data collected during this project will be published in high visibility journals. In terms of carrier perspective in Belgium, I plan to apply in the next year either to a permanent research position at the FNRS or to a research engineer position at the FNRS (to be completed in the Lab of prof. Bruno Rossion). This will allow to pursue research that was initiated in the current project.