Fast periodic visual stimulation (FPVS) to understand face perception

Contributed by Bruno Rossion (text updated June, 2014)[1]. Papers of the lab highlighted and available on the website:

http://face-categorization-lab.webnode.com/publications

Since 2010, we have been developing a research program to understand face perception by means of the **periodic** stimulation of face stimuli at a relatively fast rate. This approach relies on presenting visual stimuli at a fixed rate to elicit a brain response exactly at that frequency rate. Using this approach with electroencephalogram (EEG) is advantageous because brain activity changes very rapidly and the sampling rate of EEG is very high. Hence, the periodic frequency of stimulation can be quite high, and yet be captured by high frequency periodic responses in EEG (or MEG).

This approach is generally used under the term **"steady-state visually evoked potentials" (SSVEP)**, a term that we owe to Martin (David) Regan (1966), who extensively studied SSVEPs in response to low-level stimuli. The SSVEP approach is also used in spatial and selective attention studies, following the seminal study of Morgan et al. (1996). However, this approach has not been applied to high-level visual processes. Or, to be more accurate, SSVEP studies published before our first investigation (Rossion & Boremanse, 2011) did not vary high-level visual properties – such as face identity - at a periodic rate. Our studies on this are performed at Louvain, Belgium, and at Stanford University, in collaboration with Tony Norcia (https://svndl.stanford.edu/).

Most of the time, I like to refer to the approach as "fast periodic visual stimulation" (FPVS) rather than SSVEP. The reasons for that are briefly discussed below. The term EEG "frequency-tagging" is also used in the literature, generally when more than one frequency is used in the stimulation (a technique also developed by Martin Regan; see Regan & Heron, 1969). I recently wrote a review on this approach to measure individual face discrimination (Rossion, 2014, *Experimental Brain Research*) and discussed other recent studies in a general review on electrophysiology of face perception (Rossion, 2014, *Trends in Cognitive Sciences*).

The problem: measuring face perception

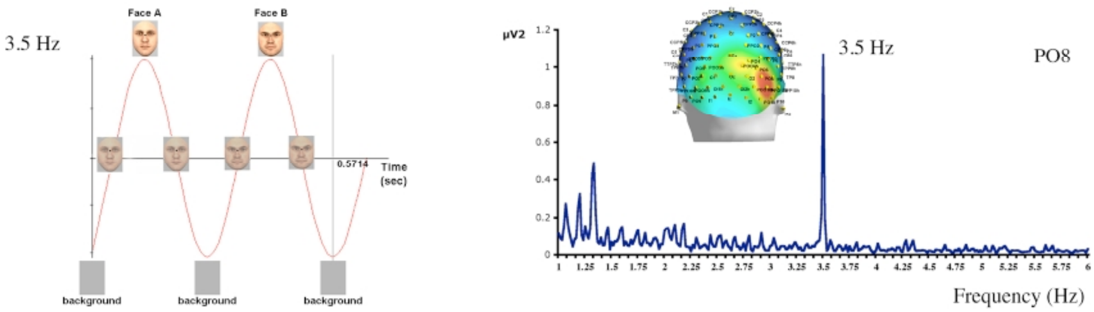
How does the human brain build a visual representation of a face to categorize this stimulus as "a face" (i.e. face detection) and discriminate it from other faces (i.e. individual face discrimination")? Despite the importance of face perception and the large amount of research on this function, it is still poorly understood. A major problem in the field of face perception is the lack of highly **sensitive** and **objective** face perception measures, i.e., measures that are not contaminated by decisional processes and which can be recorded using the same stimulation mode in all kinds of populations.

This is what FPVS provides.

[1] Author's note: this text summarizes the research program pursued in the author's laboratory (Face Categorization Lab) at the University of Louvain. It reflects the author's personal view on theoretical and methodological issues concerning face perception.

FPVS and the SSVEP

When a stimulus, or the property of a stimulus, is repeated at a fixed rate, i.e., *periodically*, it generates a *periodic* change of voltage amplitude in the electrical activity recorded on the human scalp by EEG. In ideal conditions, this EEG response is stable in phase and amplitude over time, and thus has been defined as a “steady-state” visual evoked potential (SSVEP, Regan, 1966). Since a SSVEP is a periodic response, it is confined to a specific frequency and is thus analyzed in the frequency domain instead of the time domain. The stimulus frequency f determines the response frequency-content: the response spectrum can have narrow-band peaks at frequencies that are directly related to the stimulus frequency.



SSVEPs – or steady-state visual evoked magnetic fields (SSVEFs) in MEG - have been recorded mainly to periodic changes of low-level attributes of simple stimuli: luminance, contrast, spatial frequency, color, or motion (e.g., Regan, 1966; Tyler & Kaitz, 1977; Zemon & Ratliff, 1982; Braddick et al., 1986; Norcia et al., 2002). Many studies have also used SSVEPs to investigate spatial and selective attention: an increase of attention to one of two simultaneously flickering stimuli specifically increases the response to the attended stimulus (Morgan et al., 1996; Andersen et al., 2008). In all these contexts, the SSVEP is thought to be a stable repetitive response (except for its modulation by attention), which is obtained when the exact same stimulus is repeated at a high frequency rate (i.e., roughly above 5-6 Hz, often around 10-13 Hz). A SSVEP response is traditionally thought to be located over occipital medial electrode sites (typically Oz), originating mainly from the primary visual cortex (Müller et al., 1997; Di Russo et al., 2007). It has also been proposed that SSVEP responses originate from the linear sum of transient ERPs (Bohorquez et al., 2007; Capilla et al., 2011; see Regan, 1989 for an in-depth discussion of this issue).

However, this definition of the SSVEP is arbitrarily restrictive: EEG periodic responses can be observed at slower frequency rates. In fact, as discussed below, using slower rates than 10 Hz is critical if one aims at investigating high-level rather than low-level visual processes (Alonso-Prieto et al., 2013). FPVS is a more generic term that defines the approach, rather than the assumed nature of the brain response, and this is why we use this terminology primarily. Moreover, our studies show that a fast periodic EEG response is not steady over time, i.e. it adapts, at least for high level visual stimuli and when recording over high-level visual regions.

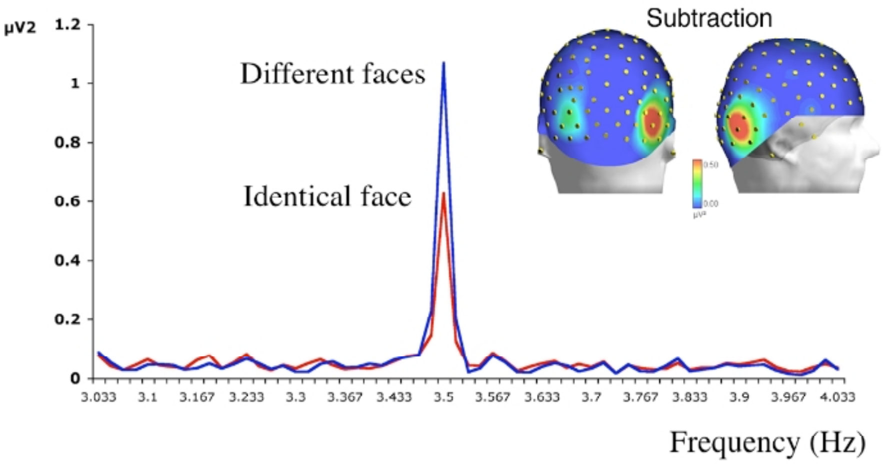
FPVS in high-level vision: a first approach for individual face discrimination

Our first study (Rossion & Boremanse, 2011) served as a proof of concept: we presented different face pictures to human observers for only one minute at a fixed rate of 3.5 Hz, namely 3.5 faces per second. See this movie: … Within only **one minute**, we found a clear EEG response confined to a narrow 3.5 Hz frequency bin, as shown in the figure above.

This response is only of about 1 μV, but its signal-to-noise ratio (SNR) – computed by dividing the amplitude at the 3.5 Hz frequency bin (the signal) with the averaged amplitude of the neighboring bins in the spectrum (the noise) - is extremely high: following only one minute of recording, the response can be 3 or 4 times larger than the response at neighboring bins (i.e., an increase of the SNR of 200%-300%).

We were quite excited when we first saw the topography of this 3.5 Hz response to faces: peaking over the right occipito-temporal cortex (channel PO8), exactly like the face-sensitive N170 component (Rossion & Jacques, 2011). This was particularly exciting since the SSVEP is thought to have a medial occipital topography, i.e. around electrode Oz. However, as we observed later this scalp topography depends on the kind of stimulus that is used AND the frequency of stimulation: at 10Hz for instance, faces do not elicit such a right occipito-temporal scalp topography (Alonso-Prieto et al., 2013).

Most interestingly, if you contrast this frequency-locked response to a response obtained when the *exact same face identity* is now repeated at a 3.5 Hz rate the SNR decreases substantially. This decrease is restricted to the frequency of stimulation and is observed only over the right occipito-temporal cortex. Hence, comparing the two conditions reveals a differential 3.5 Hz response over bilateral occipito-temporal cortices, with a right hemispheric dominance as in the figure below (Rossion & Boremanse, 2011).



The only difference between the two conditions is whether face identity varies or not at every cycle: the different faces are equalized in luminance, and there is also a substantial change of face size at every cycle (range of 82%-118% of a base face, see movie 1 in supplementary material of Rossion and Boremanse, 2011 for 4 seconds of stimulation at 3.5 Hz, i.e. 14 faces). Hence, we can safely attribute this differential response between the two conditions to the brain's discrimination of individual faces.

The originality of the present FPVS approach lies in the comparison of two conditions in which the property of interest – here, face identity - either varies periodically or remains stable at every periodic stimulation cycle. Hence, this approach differs from previous "SSVEP" studies: here, it is the property of interest that changes or remains constant at a periodic rate, the response of interest being isolated by a comparison of the two conditions.

The strengths of FPVS

Why would you use this approach? Why use EEG if you do not extract information about the timing of processes? Isn't EEG used primarily because of its high temporal resolution?

This FPVS approach should be considered, at least initially, as an alternative to behavioral measures: it measures the brain' sensitivity to a stimulus property. Of course, all information about *where* and *when* this response happens in the brain is not lost, and we'll come to that in due time. But it's not the primary goal now: the field of face perception produces hundreds of experiments and papers every year, and really needs an approach that provides highly *reliable* measures (i.e., measures that are replicable), measures that are o*bjectively* defined before and identified after the experiment, and measures that can be obtained in the absence of an explicit task and do not require overt behavioral responses. FPVS provides just that.

1. Objective FPVS provides an objective measure, namely a response at a frequency defined by the experimenter. A 3.5 Hz stimulation provides a 3.5 Hz response, and the process of interest is confined within this small frequency bin. In contrast, transient stimulation of a face leads to multiple ERP components at overlapping time-courses, or transient event-related EEG synchronization or desynchronization (ERS/ERDs) which spread over various relatively large and variable frequency bands (i.e., theta, beta, alpha, gamma range, etc.). Even when a particular component of interest is targeted (e.g., "the face-sensitive N170 component", e.g. Bentin et al., 1996; Rossion & Jacques, 2011 for review), the definition of the response of interest is highly subjective, paving the way for inadequate definition and measurement (see Rossion & Jacques, 2008).

2. Quantified The response is easily quantified: the 3.5 Hz response can be measured unambiguously, without post hoc definition of a particular time-window or a frequency band of interest. Moreover, its SNR can be computed directly.

3. Straighforward. The data analysis is extremely simple and straightforward, there are no complex data crunching procedures involved. Most of the time there is no need to correct for artefacts (blinks, etc.) because they affect frequencies unrelated to the stimulation. Hence, it's very rare to have to remove a subject's dataset because of a poor signal-to-noise ratio.

4. High SNR The response has an extremely high SNR and thus provides big effects, with only brief experiment duration. Why is the SNR so high? The main reason is that the frequency resolution is inversely proportional to the length of the EEG segment analyzed (e.g., 60 seconds: frequency resolution = 1/60 = 0.0166 Hz). Thus, the response concentrates in a very narrow frequency band containing only little noise, because the noise is distributed in many frequency bands (Regan, 1989). Moreover, one can choose a frequency that is outside of the noisy EEG frequency bands (e.g. alpha-band). The approach is thus relatively immune of artifacts, making the analysis relatively straightforward and the results highly reproducible across experiments.

5. Implicit Finally, the measure is implicit: the periodic response can be measured in the absence of an overt behavioral measure, so that it is not contaminated by decisional processes. In the example above, participants simply monitored rare nonperiodic changes of the color of a fixation cross, but were not instructed to explicitly process face identity (Rossion & Boremanse, 2011). Because of that, the approach can be used similarly in typical human adults and in populations who are unable to provide overt behavioral responses, such as infants or clinical populations.

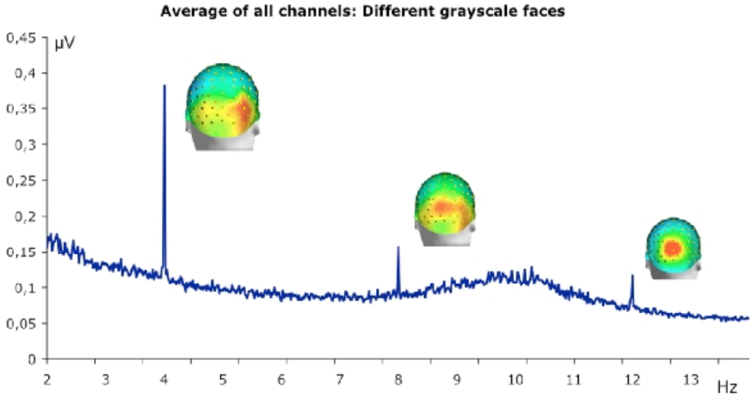
All of these characteristics of the FPVS approach make it particularly appealing for understanding a complex visual function such as face perception.

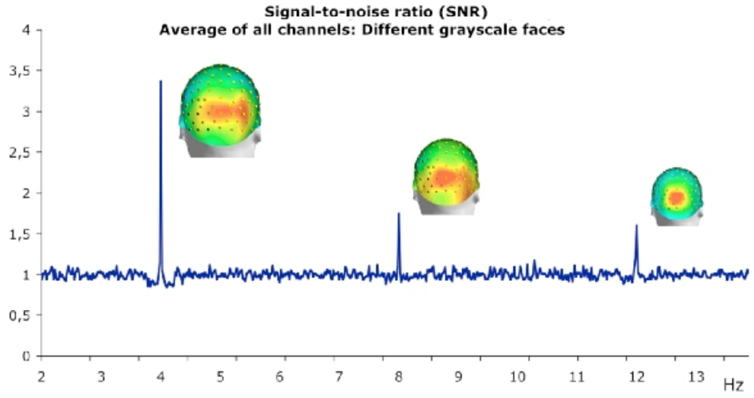
Generalization and Harmonics

How do we know that the response recorded for different faces vs. the same face at a fixed rate is a high-level response? I mean, is it not due to changes in luminance or color of the different faces compared to the same face repeated?

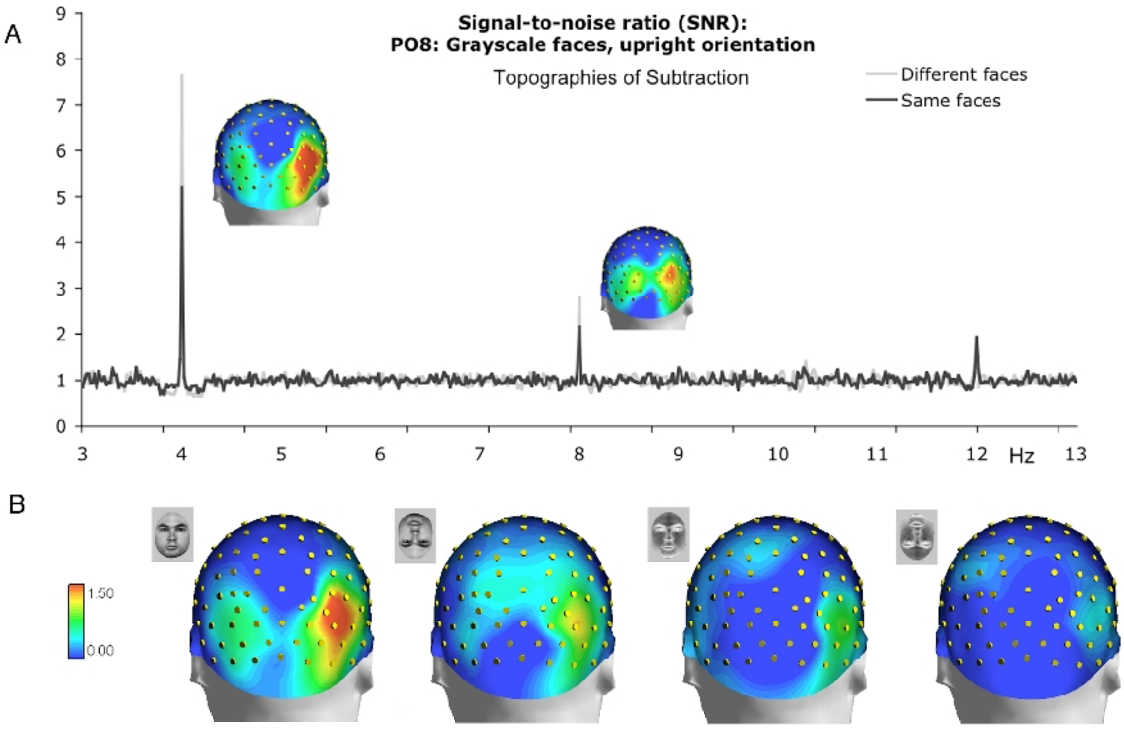
First of all, faces are equalized for luminance in our studies. Moreover, they are presented with a large change of size at every stimulation cycle, so that the images presented at every cycle *are* different.

The other properties (contrast, spatial frequency, color) are not controlled because they are part of what constitutes face identity (see Rossion, 2014, TICS, for a discussion of this issue and see also the discussion of our research projects on the N170). However, we can study the effect of these cues. For instance, we replicated the results of our first study in an experiment with grayscale faces presented at 4 Hz (Rossion et al., 2012).





In that study, we found that the large response at 4 Hz and also at the second harmonic (8 Hz), an exact integer of the 4 Hz rate, decrease for the exact same stimuli that are presented upside-down and contrast-reversed, two manipulations known to greatly disrupt face perception.



These observations show that the response obtained with FPVS is a high-level discrimination response, which reflects at least partly our specific visual expertise with faces. These observations also pave the way for investigating individual face discrimination responses to subtle stimulus manipulations.

Why do we also observe harmonics of the 4 Hz (or 3.5 Hz) face frequency rate?

When using a squarewave stimulation (abrupt periodic onset/offset), these harmonic components are present in the stimulus. However, higher harmonic components than the fundamental frequency rate are present even when the input stimulation is sinusoidal. This could be due to the double response of low-level visual processes to contrast modulation (i.e., one increase and one decrease of contrast by cycle: 4 faces but 8 changes by second). Yet, even a pure sinusoid generates frequencies in the response (the output) that are not present in the stimulus (the input), demonstrating the presence of non-linear neural mechanisms (e.g., firing threshold) (e.g., Regan, 1966; 1989). Interestingly, as shown in the figures above, when stimulating at 4 Hz, both the fundamental (4 Hz) and second harmonic response (8 Hz) are larger in amplitude over the right occipito-temporal cortex for different than identical faces (Rossion et al., 2012). Differences are not observed at higher harmonics (12 Hz, etc.), at which responses are localized over occipital medial electrode sites (Rossion & Boremanse, 2011; Rossion et al., 2012). This suggests that these responses are driven by low-level cues, which do not vary across conditions. Although a peak at the 8 Hz second harmonic in the frequency spectrum does not necessarily reflect a neural response occurring 8 times/second, these observations suggest that there is a limited bandwidth of frequencies of interest for observing individual face discrimination responses, with a high cut-off frequency somewhere in between 8 and 12 Hz. This brings the question of the suitable/optimal frequency rates to use to investigate these issues.

The frequency-tuning function of individual face discrimination

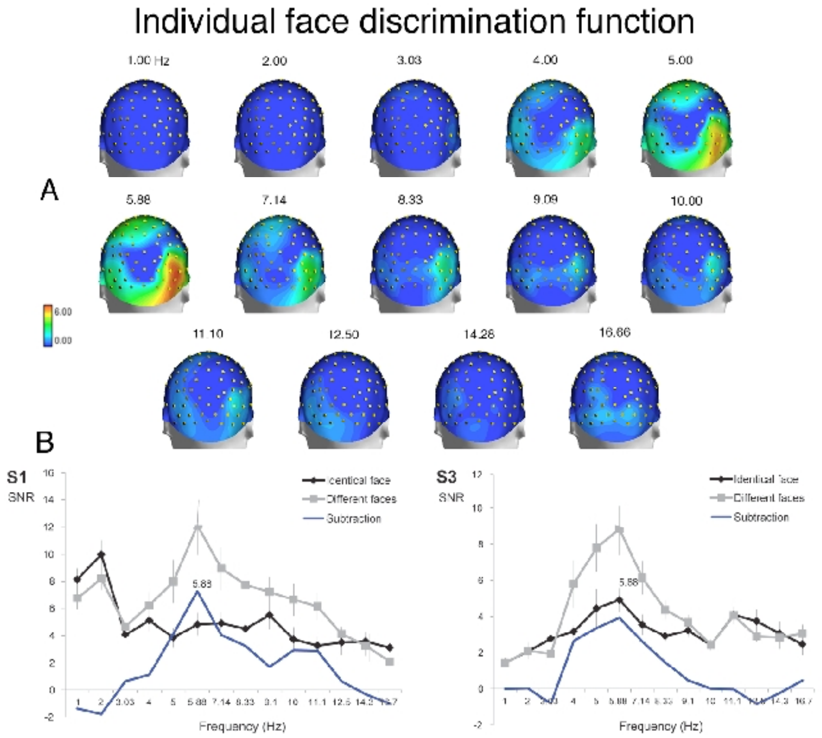
Why did we use 3.5 Hz in the first study, and which frequency rate works best?

Traditional periodic visual stimulation studies have used relatively high frequency rates, under the assumptions that a "steady brain response" requires such high frequency rates and that the "visual system's optimal frequency rate" is around 10 Hz (Regan, 1966) or 13 Hz (Silberstein et al., 1990). However, this isn't true: such relatively high frequency rate values may lead to the largest response only when stimulating with exactly identical low-level visual stimuli (i.e., luminance flicker) and when looking over low-level visual regions.

In our first study, we were not keen on using such high frequency rates because we reasoned that individual faces would not be discriminable. Then, we chose to use 3.5 Hz in reference to an excellent SSVEP study by Appelbaum and colleagues (2006), who used 3.0 Hz and 3.6 Hz for their figure and background stimuli. So to be honest, we were just lucky in that first study because if we had used 2 Hz, we would have concluded that there is no individual face discrimination response (Alonso-Prieto et al., 2013).

What are the "best" frequency rates for different faces?

To answer that question, we performed a study using 14 frequency rates between 1 and 16.66 Hz (i.e., a face every 1000 to ~60 ms): the difference between the two conditions (*different faces – identical face*) is observed for stimulation frequencies above 3 Hz and below 9 Hz, peaking at a frequency rate of about 6 Hz (5.88 Hz, Alonso-Prieto et al., 2013). We really got lucky in our first study with the 3.5 Hz …



Strikingly, despite substantial interindividual variability in SNR, the frequency tuning function is remarkably similar across individuals, peaking at right occipito-temporal sites for all suitable frequency ranges.

What do these observations mean? They indicate that there is a suitable bandwidth for individual face discrimination, centered around 6 Hz.

At rates above 8.33 Hz (cycle duration of 120 ms), there are no consistent differences between the two conditions ("same" and "different" faces). This suggests that the system does not have time to process one face at the individual level before the next face interrupts its processing. Thus, even though an observer might perceive differences among individual faces at frequency rates above 8.33 Hz, his/her face perception system cannot synchronize to, i.e., process, *every* single face that is presented in the sequence. These results therefore provide original information about the *temporal bottleneck* of individual face discrimination in humans: *at least 120 ms is necessary to process a face at the individual level, and a duration of 170 ms (5.88 Hz) seems to be sufficient for a full individualization process*.

The absence of a repetition suppression effect at low frequency rates (below 3 Hz) may be due to a too long interstimulus interval between individual faces: information about a repeated individual face may remain present in the neural response for no more than 250-300 ms, and disperse thereafter. Alternatively, the absence of effect at low-frequency rates may be because 'transient' ERP components are clearly distinguishable, since there is time to return to baseline before the next stimulus arrives. Differences between conditions may thus take place on successive components of different polarities (e.g., P1, N170, P2, N250, etc.), so that the overall difference between conditions may be cancelled out when measured on the scalp (see Figure 7 in Alonso-Prieto et al., 2013).

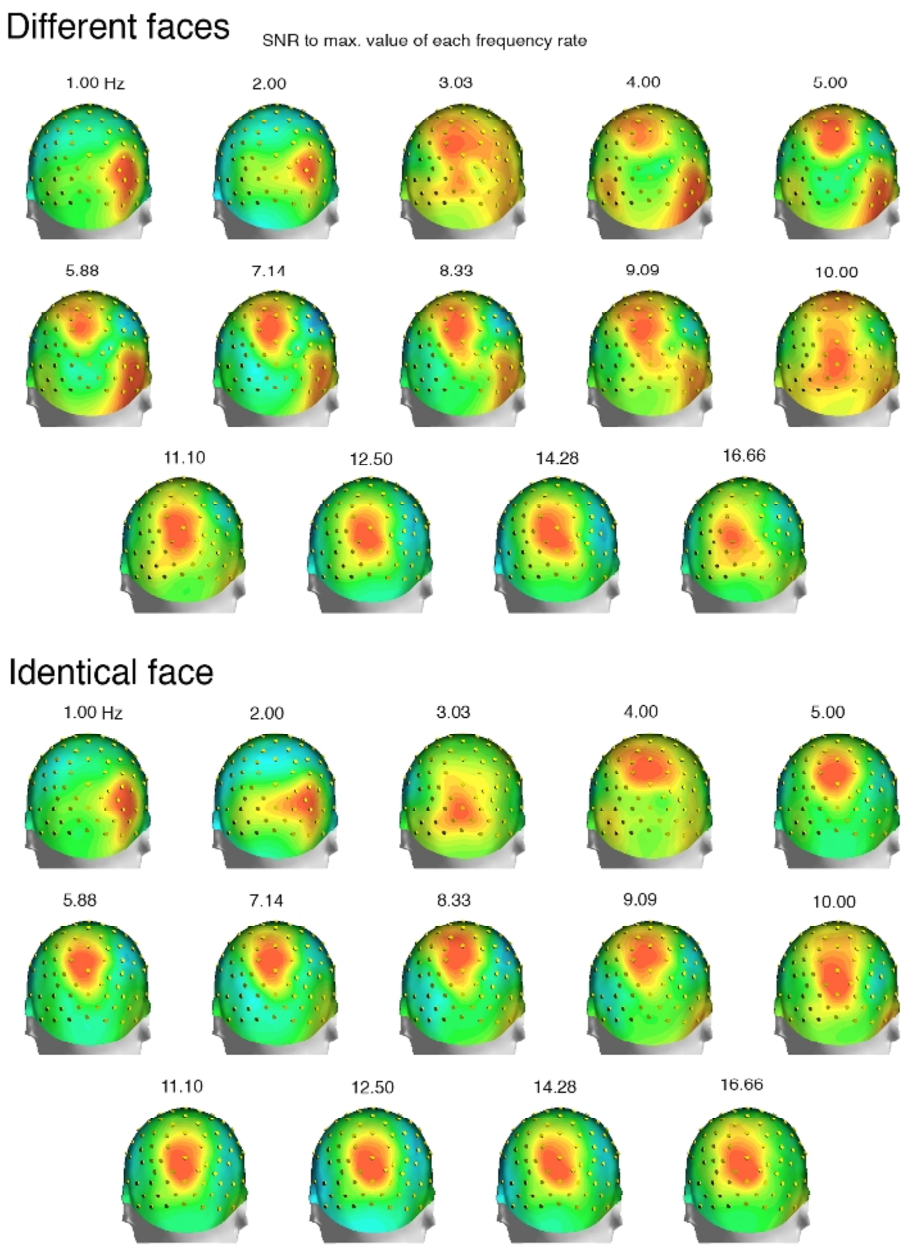
Irrespective of the correct explanation, it seems that for complex visual stimuli such as faces, frequency rates above 3 Hz – i.e. when there are no clearly identifiable successive ERP components – must be used to provide visual discrimination responses at the periodic frequency of stimulation. Hence, although the term "fast" in FPVS is relative, it is informative: a relatively fast rate of visual stimulation is indeed necessary to capture some of the phenomena of interest such as individual face discrimination.

Now, this is not the end of the story … the figure on the next page is interesting because it shows the scalp distribution for each of the conditions separately (same or different faces).

What we see there is that the range of very low stimulation rates for classical ERP studies (i.e. < 1 Hz) *and* the very high range of stimulation for classical SSVEP studies (i.e. > 10 Hz) are inadequate, or suboptimal suboptimal to study individual face discrimination!

Below 1 Hz, faces elicit primarily a response over the right occipito-temporal cortex. However, this response is not sensitive to a change of face identity at every stimulation cycle. Above 10 Hz, the response becomes centered over medial occipital sites and does not vary with the change of face identity. Hence, the optimal range of temporal frequency rate for individual face discrimination appears to be between 3 and 8.33 Hz: stimulating at this temporal frequency may help to isolate face-specific processes. This leads to interesting predictions for behavioral studies, which we have started to explore.

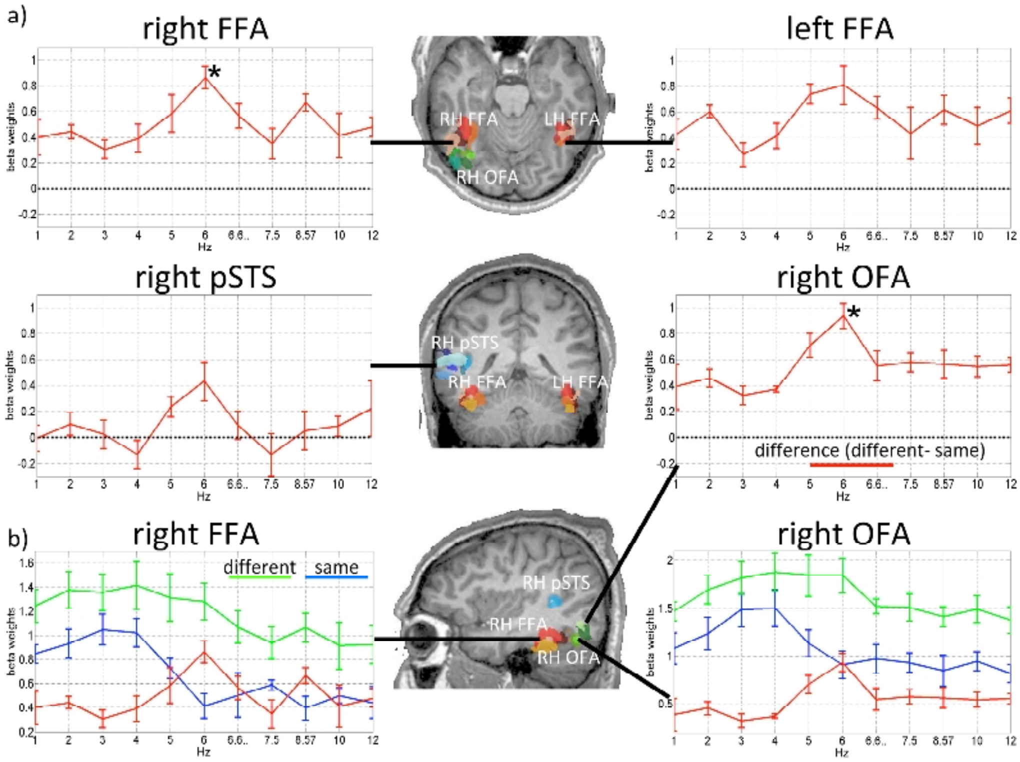
This figure also shows that characterizing a frequency-tuning function for high-level visual stimuli such as faces *requires* using *different faces* at every stimulation cycle: otherwise, the response is centered over medial occipital or medial occipito-parietal sites at most frequency rates.



Frequency-tuning of individual face discrimination in human fMRI

What is the relevance of this 6 Hz frequency-tuning function? Maybe it's just due to the peculiarity of the EEG technique?

To test that, we performed a similar frequency-tuning experiment in fMRI (Gentile & Rossion, 2014). Of course, with a slow temporal resolution method, such as fMRI, the response measured, i.e., the differential blood oxygen level-dependent (BOLD) signal between blocks of different faces compared to the same repeated face, cannot be specific to the frequency of stimulation. Yet, interestingly, considering only the magnitude of the BOLD response over several seconds, the frequency-tuning function obtained with fMRI in face-selective areas of the occipito-temporal cortex is similar to the function obtained with EEG, peaking also at 6 Hz (Gentile and Rossion, 2014).



These face-selective regions include the so-called fusiform and occipital “face areas” (FFA and OFA), as well as the posterior temporal sulcus (pSTS). In fMRI, though, this effect is due both to a maximal response to different faces in a range of 3 to 6 Hz and to a sharp drop of the BOLD signal from 6 Hz onward when the same face is repeated during a block. These observations complement the EEG observations by providing a neural basis of the effect observed on the scalp, indicating that face-selective cortical areas process each individual face in full when these successive faces are presented every 160-170 ms.

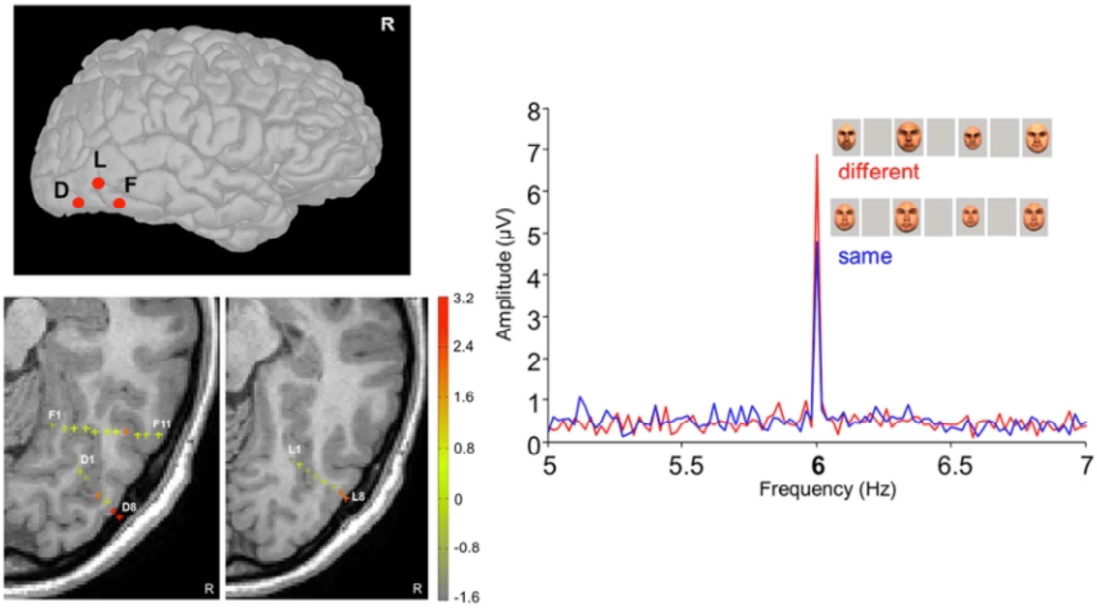
Yet, in fMRI, differences between the two conditions remain significant at slow (< 3 Hz) and high rates (> 9 Hz) in most functional areas (Gentile and Rossion, 2014). This discrepancy with the EEG results suggests that at high stimulation frequency rates the system bypasses some of the different faces presented in succession: the fMRI effect – but not the EEG effect - can be driven by the perception of only a *subset* of different faces during a block.

The discrepancy with EEG suggests therefore that these fMRI effects occur at a different time-scale than the exact rate of stimulation. Nevertheless, *this relatively slow rate appears to be suboptimal to disclose large repetition suppression effects*. Also, such rates may be too slow to disclose individual face repetition effects related to individual face discrimination in regions such as the pSTS, which is tuned to rapidly changing (i.e., dynamic) stimuli (Puce et al., 1998; Schultz and Pilz, 2009).

Does it mean that all these face-selective regions contribute to the periodic EEG response record on the scalp?

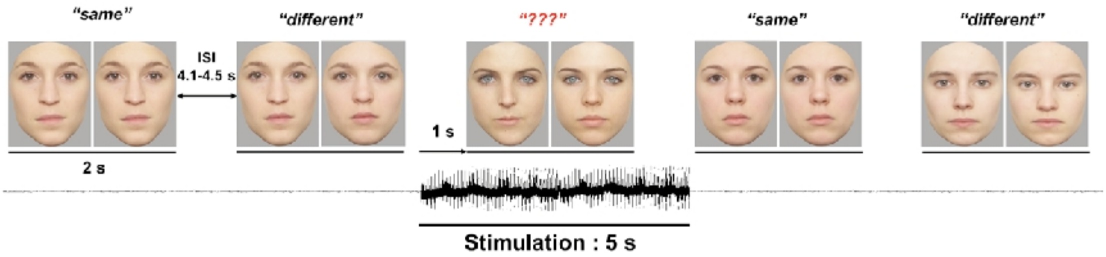
Possibly, or probably, although the relationship between the BOLD response and electrophysiological responses observed exactly at the stimulation rate remains unknown. The answer to this question is more likely to come from recordings of intracerebral responses with this approach, something that we have started to explore in collaboration with Louis Maillard and his colleagues in Nancy (stereotactic EEG, SEEG).

Very recently, we had the opportunity to test an epileptic patient implanted with 3 rows of electrode contacts inserted in the right inferior occipital and posterior fusiform gyrus. Face-selective responses were recorded on several contacts of one electrode in particular (D), close to the cortical surface and in the so-called right "occipital face area". At these electrode contacts we observed robust effects of repetition suppression exactly at a 6 Hz periodic stimulation, these effects being significantly reduced for inverted faces (Jonas et al., in press). Hence, this region is indeed very likely to contribute to the efefct observed on the scalp.



But does this kind of effect reflect functional processes?

Yes. It turns out that when stimulating electrically the electrode contact at which we observed the largest repetition suppression effect, in the right "occipital face area" (OFA), the patient makes mistakes at an individual face discrimination task: she fails to see two different faces presented simultaneously as being different ! Without stimulation, or when stimulating at other electrode sites, the patient KV is in fact very good at this task (Jonas et al., in press)***.*** This observation suggests that the region where this electrode contact is recorded is critical for individual face discrimination, linking the intracerebral EEG effect obtained with periodic stimulation to a critical function.

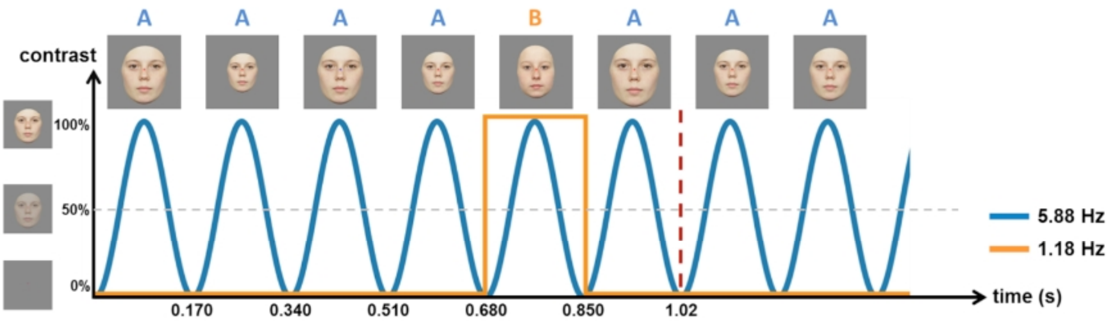


Back on the surface now … How can I use this technique to measure a visual discrimination response even more directly, i.e. without having to compare the response obtained for different conditions (i.e. at different times)?

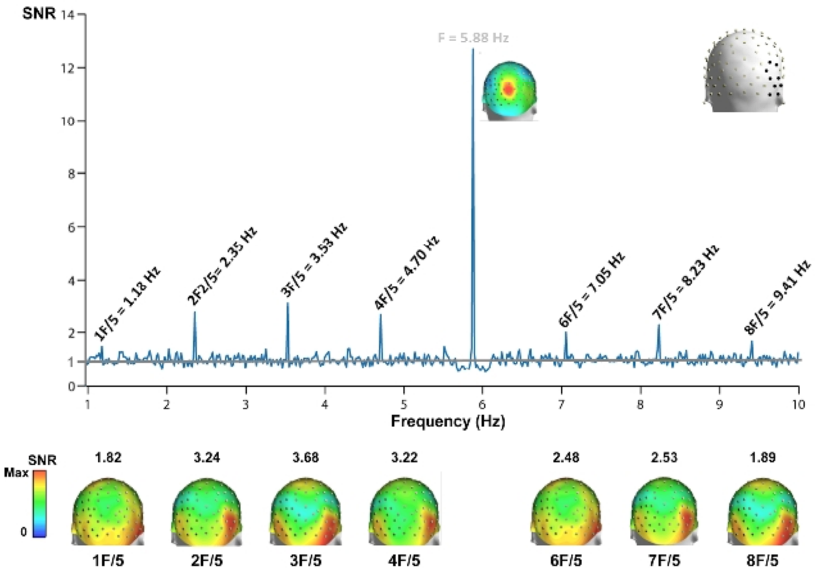
Fast oddball face discrimination

To do that, we took the fast oddball periodic stimulation approach developed by Braddick et al. (1986) and Heinrich et al. (2009) for low-level stimuli to extend it to high level vision.

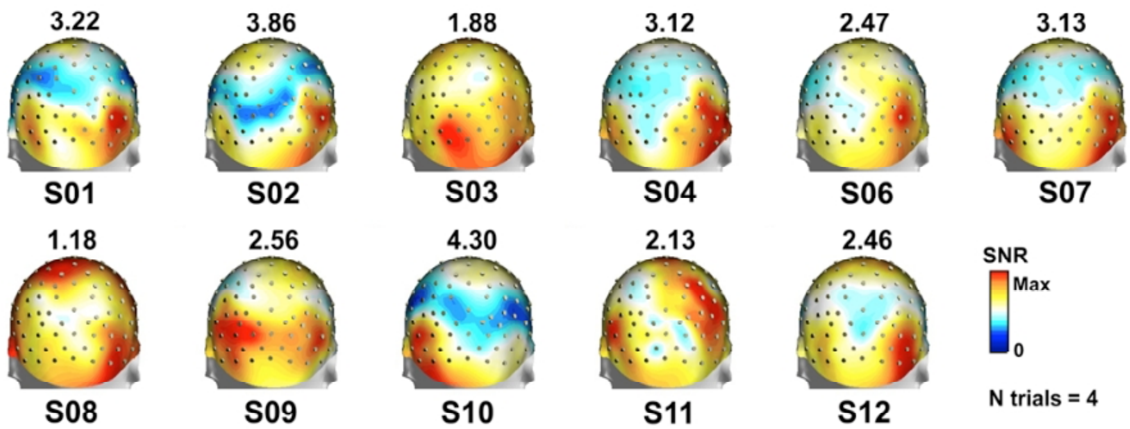
In a first study, we presented the same face (A) at a 5.88 Hz frequency (base frequency *f*) for 60 s, and introduced different *oddball* faces (B, C, D…) every 5th base face, i.e., at an oddball frequency of 1.18 Hz (= *f*/5 = 5.88 Hz/5) (Liu-Shuang et al., 2014; see movie 2 in supplementary material of that paper or check our website for such movies: *http://face-categorization-lab.webnode.com/products/aaab-stimulation/*).



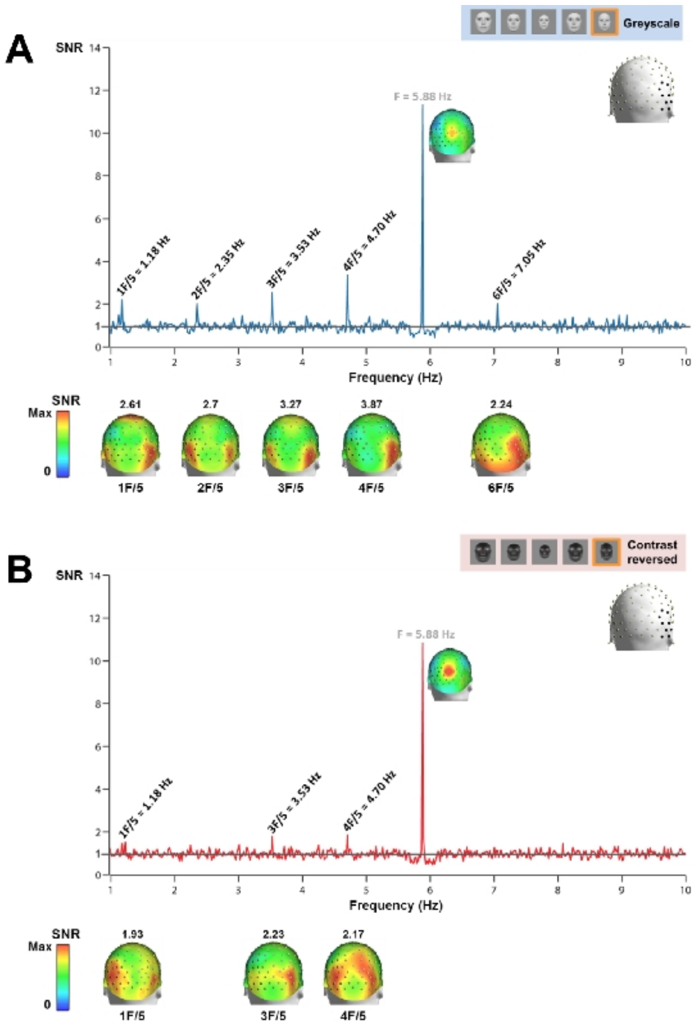
In these conditions, a robust measure of individual face discrimination is observed at the exact frequency at which face identity changes (every 850 ms, or 1.18 Hz) and at its harmonics (i.e., 2*f* = 2.35 Hz, etc.). This response is localized over the right occipito-temporal cortex and differs from the large response at the base frequency, peaking over medial occipital sites (Oz).



The discrimination response can be obtained rapidly in individual brains, without asking participants to explicitly attend to the faces. Just look at this figure below, showing the SNR and topographical maps of individual face discrimination data in individual participants… following only 4 minutes of stimulation !



When the exact same faces are presented upside-down or with their contrast reversed, the individual face discrimination response at the oddball frequency is substantially reduced. However, importantly, the response at the base frequency remains unaffected (Liu-Shuang et al., 2014).



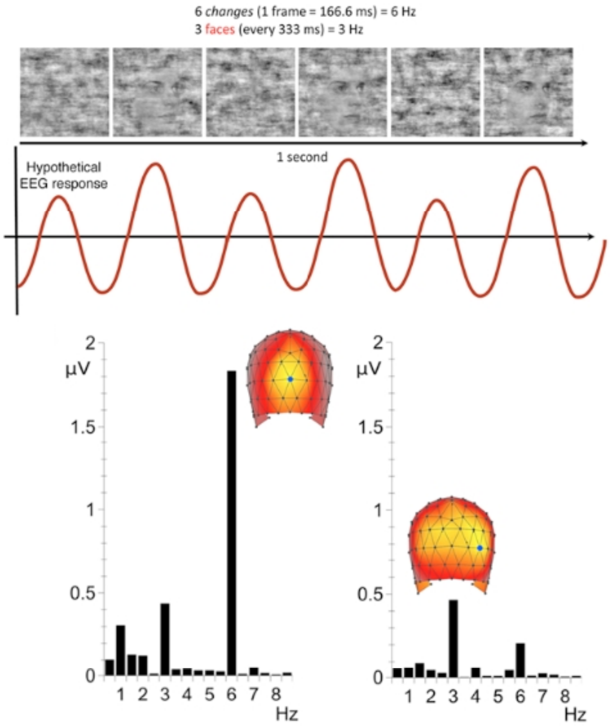
This fast oddball periodic paradigm maintains all the advantages of the FPVS approach (objectivity, speed and simplicity of data processing, sensitivity, implicit measure) and can isolate a discrimination response without relying on a subtractive operation between separately recorded conditions. Instead, a periodic response at the oddball frequency is already a measure of a difference in response to the base and oddball stimuli, and a significant response at the oddball frequency is sufficient in itself to infer visual discrimination.

We are currently exploring other face discrimination functions with this approach, which has great potential for the characterization of face perception impairments in clinical populations, or in the development of face perception abilities.

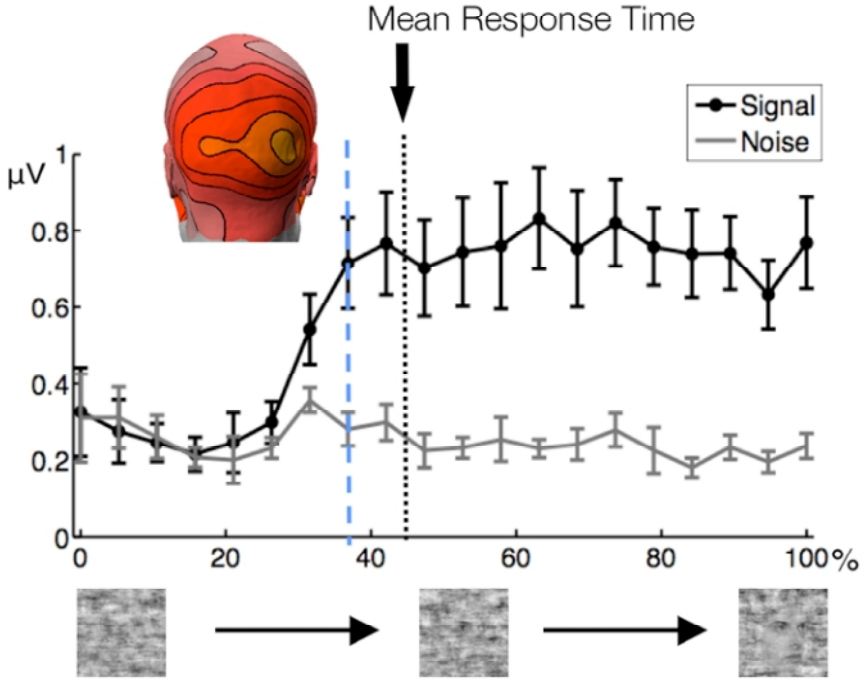
Robust and objective face detection thresholds

In a different line of research with the FPVS technique, we collaborate with Tony Norcia and his laboratory at Stanford University to develop powerful paradigms to measure face perception thresholds. This approach takes another of Regan's inventions, the sweep VEP paradigm (Regan, 1973), in which a stimulus property (contrast for instance) increases or decreases periodically.

In a first study (Ales et al., 2012), 120 phase-scrambled face stimuli are presented over a series of 20 equally spaced steps during a 20 second sequence (i.e., 6 stimuli/second). This sequence generates a robust EEG response exactly at the 6 Hz stimulation rate over low-level visual regions (medial occipital sites). Derandomization of the phase spectrum of every other stimulus leads to the presentation of 3 faces by second and a robust 3 Hz response over the right occipito-temporal electrodes.



Now… let's sweep… progressively derandomizing the phase shows that this objective signature of face detection emerges abruptly between 30% and 35% phase-coherence of the face. This 3 Hz response occurs before the behavioral face detection response and is predictive of this response.



Using this procedure, thresholds for face detection can be estimated reliably in single participants from 15 trials only (5 minutes of total recording), or on each of 15 individual face trials across 10 participants (Ales et al., 2012). Although this approach does not provide information about the precise time-course of face detection, it takes advantage of the high temporal resolution of EEG, allowing the isolation of specific responses at high frequency rates, to provide sensitive and objective visual perception threshold measures. Thanks to these advantages, it also opens an avenue to measure and compare various face discrimination functions in different human populations, including infants and individuals with developmental delay. We are currently extending this approach to test its specificity to faces and neural basis.

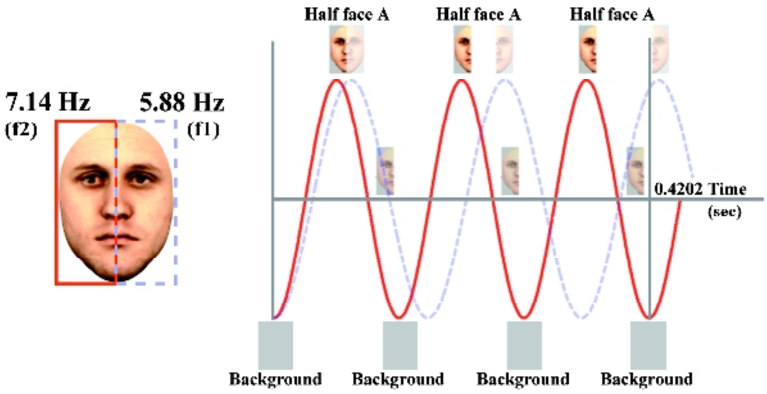
All right, all of this is interesting … this looks like a powerful tool but what have we learned that we did not know? How can you use the technique to address issues that cannot be resolved with other approaches?

Objective evidence for holistic representation of faces

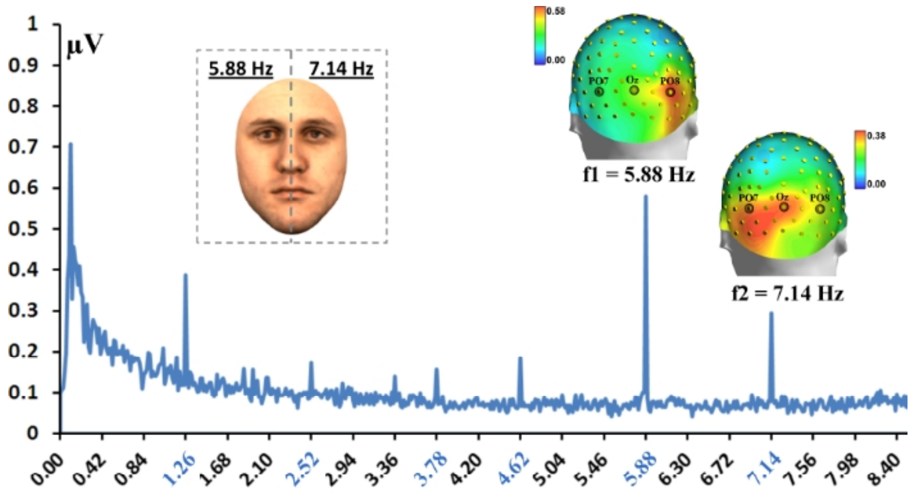
An outstanding issue in face perception research concerns the nature of the face percept: *is it based on independent facial parts or on an integrated unit, a so-called "holistic/configural" representation? How can we objectively dissociate part-based and holistic face representations?*

This issue is very difficult to resolve with conventional methods. Presenting a face part alone (i.e. a subset of a whole face) can trigger the activation of the whole face representation, and presenting two parts leads to a brain response that cannot be objectively dissociated into a representation of each of the parts.

To circumvent this problem, we used the frequency-tagging approach, yet another invention of Martin Regan (Regan & Heron, 1969), that has been used mainly in studies of spatial and selective attention (e.g. Morgan et al., 1996). Specifically, we contrast-modulated the left and right halves of a face stimulus with different frequencies (5.88 and 7.14 Hz) (Boremanse, Norcia & Rossion, 2013).



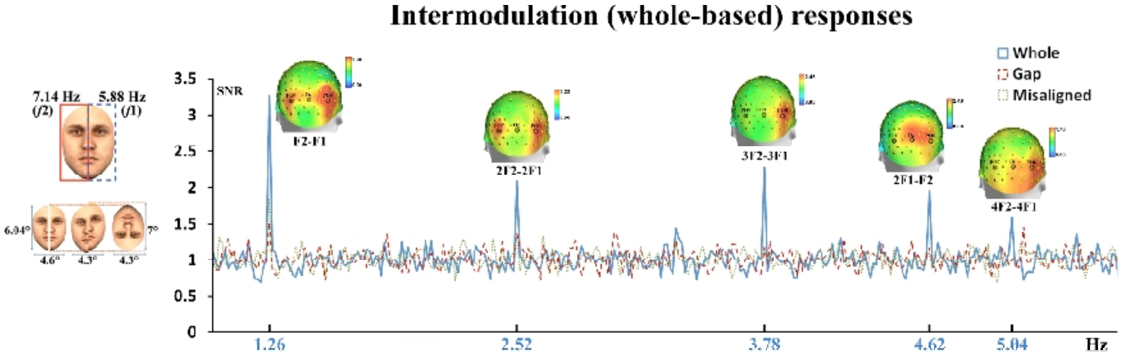
In doing this, we were able to obtain two separate responses that could be unambiguously assigned to each of the facial halves.



Hence, this approach is able to simultaneously measure an independent neural response to each face part !

Most interestingly, responses corresponding to exact differences between the two input frequencies (e.g., 7.14 – 5.88 = 1.26 Hz, etc.) can be observed. These intermodulation (IM) responses between the two frequencies are not present in the stimulus, they are generated by the system (nonlinearities) and can only arise from neuronal populations that integrate the two inputs nonlinearly (Zemon & Ratliff, 1984; Regan & Regan, 1988).

In our study, these IMs are prominent over right occipito-temporal channels, suggesting the presence of high-level integration processes of the two face halves.

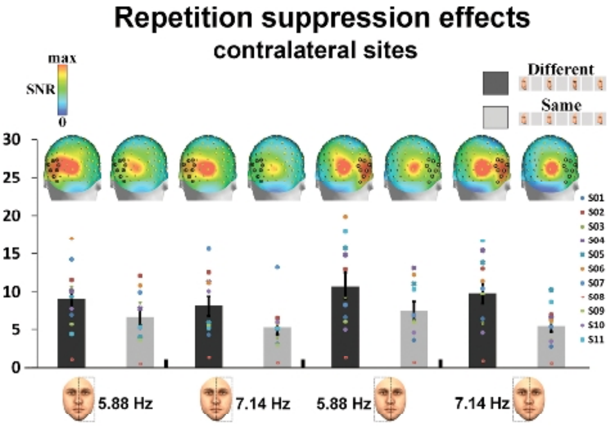


Importantly, manipulations breaking the whole face into its constituent parts, such as spatial separation by a gap, vertical misalignment, or even inversion, reduces dramatically the IM responses, but the part-based fundamental frequencies (5.88 Hz and 7.14 Hz) responses remain unaffected. Thus, we argue that the IM responses identified in the EEG provide the first objective signature of an integrated (i.e., “holistic/configural”) face percept and a dissociation with part-based responses.

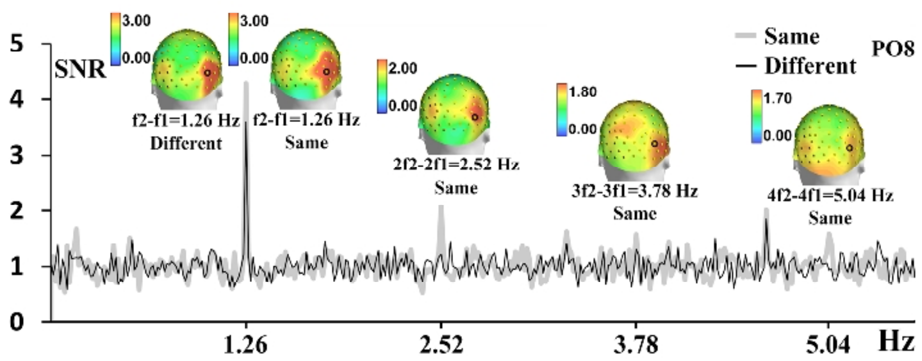
Can we further dissociate part-based and holistic face representations?

Yes. We recently replicated this study in full by adding one manipulation: repeating the same facial halves at every cycle decreased the part-based EEG responses (i.e. 5.88 Hz and 7.14 Hz) as compared to when the face parts changed identity at every cycle (Boremanse et al., in press). Thus, we were able to find part-based face repetition effects: again, something that one cannot do by presenting a single part alone.

Interestingly, these part-based repetition suppression effects did not depend on the structure of the face: they were equally large when the parts were spatially separated, or the face was inverted. Moreover, increasing the response to face parts by changing identity at every stimulation cycle decreased the IM components, showing that these two kinds of responses – reflecting part-based and holistic representations - are objectively separated in the system (Boremanse et al., in press).



Intermodulation components



All right, time to wrap this up … this is an ongoing research program and there

see our publications (please find selected summaries below) for more in depth discussion of these findings.

<u>BIBLIOGRAPHY (lab papers) and main finding(s) of each paper</u>

http://face-categorization-lab.webnode.com/publications

Any comment about this text? Please email bruno.rossion@uclouvain.be

1	Rossion, B. & Boremanse, A. (2011). Robust sensitivity to facial identity in the right human occipito-temporal cortex as revealed by steady-state visual-evoked potentials. *Journal of Vision*. 11(2):16, 1–21. *The first study of our group using fast periodic visual stimulation. Other recent studies have used face stimuli to record SSVEPs, but the originality of this study is that the property of interest – face identity –varies at the periodic frequency rate. We found a much larger response at 3.5 Hz, over the right occipito-temporal cortex, when face identity changes at that rate than when identity does not change. This study only had one minute of stimulation for each condition and served a proof of concept to show that the technique worked. We also showed no difference between the conditions when faces were presented upside-down.* **Paper first submitted to *JOV***
2	Rossion, B., Prieto, E.A., Boremanse, A., Kuefner, D., Van Belle, G. (2012). A steady-state visual evoked potential approach to individual face perception: effect of inversion, contrast-reversal and temporal dynamics. *NeuroImage*, 63, 1585-1600. *This is an extension of the Rossion & Boremanse (2011) study, in which we used 4 Hz instead of 3.5 Hz, and, more importantly, showed that the increased 4Hz response to different rather than identical faces was not due to color, using grayscale faces. Moreover, inversion and contrast-reversal of the faces led to a*

	severe decrease of the 4 Hz right occipito-temporal response, and a delay of the phase of the response. Finally, this study looked at the temporal dynamics of the modulation of the response by the change of identity: following a 15 second baseline with the same face, an abrupt change of facial identity led to a release of activity confined to the 4 Hz stimulation frequency. **Paper first submitted to *NeuroImage***
3	Ales, J., Farzin, F., Rossion, B., Norcia, A.M. (2012). An objective method for measuring face detection thresholds using the sweep steady-state evoked response. *Journal of Vision,* 12:18, 1-18. *The first use of the "sweep VEP" approach invented by Regan (1973) with high level visual stimuli. "Sweep" means that the property of interest increases or decreases progressively, in order to monitor the emergence or disappearance of the periodic response of interest. The trick here was to alternate phase-scrambled stimuli at 6 Hz (i.e., changing the phase-randomization 6 times/second) and progressively descrambling the phase of every other stimulus to elicit a 3 Hz face-related response. We found significant 3 Hz responses emerging over the right occipito-temporal cortex at 30-35% of phase coherence, before behavioral face detection. With only 15 different faces by subject, we were able to derive an objective threshold for face detection, predicting variability in behavioral performance across the variable face stimuli. The phase-scrambling algorithm developed by Justin Ales for this study ensures a strictly linear decrease of the phase-randomization, unlike previous procedures.* **Paper first submitted to *JOV***
4	Alonso-Prieto, E.A, Belle, G.,V. Liu-Shuang, J., Norcia, A.M., Rossion, B. (2013). The 6 Hz fundamental frequency rate for individual face discrimination in the right occipito-temporal cortex. *Neuropsychologia*. 51, 2863-2875. *We studied the frequency-tuning function for individual face discrimination by comparing the responses to trains of identical or different faces at periodic rates between 1 and 16 Hz. In all 4 observers, significant effects were found between 3 and 8.3 Hz, and there was a similar differential frequency-tuning function, with the largest difference at 5.88 Hz, or about 6 faces/second. From these results, it seems that a rate of 5.88 Hz is optimal for discriminating individual faces: the face processing system has time to process each individual face before the next one comes in. At higher frequency rates, there is not enough time. This study has practical consequences, providing information about the rates to use to disclose the most robust effects of individual face discrimination. It also provides original information not about the time it takes for facial information to reach the system, but the time it takes for a face to be processed at the individual level (i.e., about 1000/5.88 = 170 ms).* **Paper rejected after review in *Cerebral Cortex,* no opportunity to respond. Not even reviewed in *Neuroimage*, then submitted to *Neuropsychologia* and accepted after constructive reviews.**

5	Boremanse, A., Norcia, A.M., Rossion, B. (2013). An objective signature for visual binding of face parts in the human brain. *Journal of Vision*, (11):6, 1-18. *The first EEG frequency-tagging experiment with facial parts. This frequency-tagging approach is yet another Regan invention (Regan & Heron, 1969) that has been used mainly in studies of spatial and selective attention. Here, we contrast-modulated the left and right halves of a face stimulus with different frequencies (5.88 and 7.14 Hz) to obtain two separate responses that could be unambiguously assigned to each of the facial halves. One cannot do that with conventional measures: it is impossible to disentangle the neural response of each part when they are presented simultaneously. Moreover, presenting only a single half of a face, for instance, may recruit the whole face representation. The most important finding was the presence of intermodulation responses (e.g., 7.14 – 5.88 = 1.26 Hz) at frequencies that were not present in the stimulus, indicating a combination of the two frequencies at a certain stage of processing in the system. Strikingly, these IMs – but not the part-based responses at 5.88 and 7.14 Hz – disappeared when the two face halves were spatially separated, and decreased when the face was inverted. The results are crystal clear, obtained in two experiments with 27 subjects in total. We take these observations as the first evidence of an integrated holistic face representation in the human brain.* **A previous version of this paper was sent to several "high impact factor" journals, but they were not interested enough to even send it for review… A very frustrating experience. A publication in *JOV*, after a thorough and fair review, allowed us to discuss more extensively the implications of these findings.**
6	Liu-Shuang, J., Norcia, A.M., Rossion, B. (2014). An objective index of individual face discrimination in the right occipito-temporal cortex by means of fast periodic oddball stimulation. *Neuropsychologia*, 52, 57-72. *Here we moved from our previous fast periodic stimulation studies that presented different conditions in separate blocks to an oddball paradigm in which the same face is presented at a fast periodic rate (5.88 Hz) with different oddball faces appearing every five faces. Thanks to this stimulation mode, we identify robust individual face discrimination response at the oddball rate (5.88 Hz/5 = 1.17 Hz and harmonics) without performing any subtraction. This individual face discrimination response is located primarily over the right occipito-temporal cortex and is significant in individual participants after a single one minute sequence. Moreover, while the base rate response is unaffected, the oddball response decreases substantially following inversion and contrast-reversal. It's an excellent paradigm to use for studying visual discrimination responses directly (no subtraction), objectively and rapidly. We have been using this approach with various manipulations of facial cues in recent studies in the lab.* **Paper rejected in *Cerebral Cortex* after 4 months and possibility to resubmit and start from scratch … went to *Neuropsychologia* instead.**
7	Gentile, F., Rossion, B. (2014). Temporal frequency tuning of cortical face-sensitive areas for individual face perception. *Neuroimage*, 90, 256-265.

	This study was inspired by the EEG study of Alonso-Prieto et al. (2013) in which we found that the largest difference between periodic stimulation of different and identical faces was at about 6 Hz. We tested whether this observation could be generalized to fMRI. The idea here was not to find a response at 6 Hz, which is impossible given the sluggishness of the BOLD response. Rather, we compared the average BOLD response to blocks of different and identical faces presented at frequency rates between 1 and 12 Hz. We found a repetition suppression/adaptation effect across all stimulation frequency rates, but the magnitude of the effect showed a typical Gaussian-shaped tuning function, peaking on average at 6 Hz for all face-sensitive areas of the ventral occipito-temporal cortex, including the fusiform and occipital "face areas" (FFA and OFA), as well as the superior temporal sulcus. These observations complement the EEG findings (Alonso-Prieto et al., 2013), indicating that the cortical face network can discriminate each individual face when these successive faces are presented every 160–170 ms. They also have important practical implications, allowing investigators to optimize the stimulation frequency rates for observing the largest repetition suppression effects to faces and other visual forms in the occipitotemporal cortex. For instance, the pSTS appears to be sensitive to individual face repetition only at around 6 Hz… **Paper rejected after review in *J. Neuroscience*, no opportunity to respond, then submitted to *Neuroimage*.**
8	Boremanse, A., Norcia, A.M., Rossion, B. (in press). Dissociation of part-based and integrated neural responses to faces by means of EEG frequency-tagging. *European Journal of Neuroscience*. *A replication of our first EEG frequency-tagging study (Boremanse, Norcia & Rossion, JOV) in which we added an important manipulation: the two face halves could change identity at every stimulation cycle (5.88 or 7.14 Hz). This led to a particularly interesting observation: repeating the same facial halves at every cycle decreased the part-based EEG responses (i.e., 5.88 and 7.14 Hz), as compared to when the face parts changed at every cycle, identifying part-based face repetition effects for the first time. However, the intermodulation responses e.g., 7.14 – 5.88 Hz = 1.26 Hz) decreased when facial parts changed identity at every cycle. This decrease provides yet another dissociation between part-based and holistic (i.e. integrated) responses to faces in the human brain.* **Paper first submitted to *European Journal of Neuroscience***
9	**REVIEW:** Rossion, B. (2014). Understanding individual face discrimination by means of fast periodic visual stimulation. *Experimental Brain Research*, 232, 1599-1621. *A review of the FPVS approach as applied to individual face discrimination. The sweep and frequency-tagging studies are not discussed in this review, which concentrates on illustrating how the approach can be used to obtain objective and sensitive measures of individual face discrimination.*

	Paper first submitted to *Experimental Brain Research*
10	**REVIEW:** Rossion, B. (2014). Understanding face perception by means of human electrophysiology. *Trends in Cognitive Sciences*, 18, 310-318. *This is not a review of the FPVS approach, but the paper summarizes research on the N170 component that as dominated this field for two decades, and suggests that a growing role will be played by periodic stimulation of faces and frequency-domain analyses, in particular for estimating face perception thresholds and capturing holistic face representations.* **Paper first submitted to *TICS (invitation)***
11	Jonas, J., Rossion, B., Krieg, J., Koessler, L., Colnat-Coulbois, S., Vespignani, H., Jacques, C., Vignal, J.-P, Brissart, H., Maillard, L. (in press). Intracerebral electrical stimulation of a face-selective area in the right inferior occipital cortex impairs individual face discrimination. *NeuroImage*. *The paper reports the second electrode implantation of the patient KV (first reported in Jonas et al. 2012). The patient had 3 electrodes implanted in the right occipital and ocicpito-temporal cortex, and we recorded EEG responses to periodic stimulation at 6 Hz inside the brain. We showed a large repetition suppression effect, significantly larger for upright than inverted faces, in a face-selective area of the right inferior occipital cortex (the right OFA). Electrical stimulation of the electrode contact showing the largest repetition suppression effect caused a transient inability to discriminate pictures of faces presented simulatenously to the patient. These findings provide original evidence for a causal relationship between the face-selective right inferior occipital cortex and individual face discrimination. More generally, they support the functional value of electrophysiological repetition suppression effects, indicating that these effects can be used as an index of a necessary neural representation of the changing stimulus property.* **A previous version of this paper was sent to several "high impact factor" journals, but was not sent for review. Sent for review at *Journal of Neuroscience*, and rejected, no option to respond. Submitted to *NeuroImage* next.**