### The N170: understanding the time-course of face perception

Bruno Rossion (text updated, July 2015)1

http://face-categorization-lab.webnode.com/research/time-course-of-face-processing-the-n170/

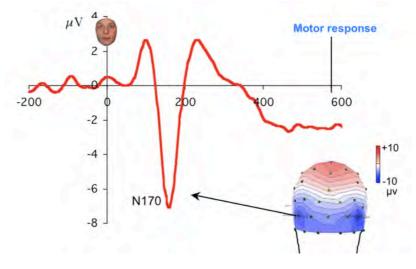
The general goal of our research is to clarify the mechanisms of face recognition in the human brain. **Recording event-related potentials** (**ERPs**) on the human scalp can be particularly informative for this goal. Because of their excellent time resolution, ERPs can help tracking face processes as they unfold over time.

#### The N170 component: introduction and background

Flashing a face stimulus to a human observer elicits a series of electrical responses on the scalp. These small changes of the electroencephalogram (EEG) that are time-locked and phase-locked to the stimulus onset are the ERPs. They vary in polarity (positive or negative), latency, amplitude and scalp topography. They are of different durations or width also, which can be expressed in frequency ranges.

ERPs can be extracted from the background EEG noise by applying the same kind of stimulation repeatedly, and averaging all the time segments (Dawson, 1951) that follow the onset of the face stimulus.

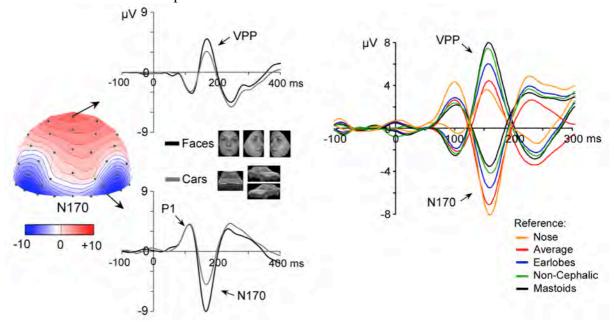
The sudden onset (flash) of a face stimulus elicits a particularly large negative component on the adult human scalp, most prominent on lateral occipital or occipitotemporal sites, peaking at about 170 ms (usually slightly earlier than that). Although it is fair to say that it was also reported in other studies at about the same time (Bötzel et al., 1995; George et al., 1996), this component has been termed the **N170** by Bentin and colleagues (1996), the first study to focus on this component and in which 5 experiments were performed to characterize its response properties.



<sup>1</sup> Author's note: this text summarizes the research and research program pursued in the author's laboratory (Face Categorization Lab) at the University of Louvain. It is not meant to provide a review of the literature on electrophysiology of face perception or the N170 in particular. The text also reflects the author's personal view on theoretical and methodological issues concerning this topic.

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Importantly, this posterior component coincides in time with a positive component maximal in amplitude at centro-frontal sites, the Vertex Positive Potential (VPP) described earlier by Jeffreys (1989; 1996). Jeffreys thought that the VPP and the negative counterparts observed on occipito-temporal sites reflected the two opposite sides of dipolar responses, and that the VPP had its origin in occipito-temporal regions. With Carrie Joyce, we have shown, indeed, that the two components reflect opposite sides of the same configuration of generators, varying inversely in amplitude with the location of the reference electrode on the scalp (Joyce & Rossion, 2005). It does not mean that there is only a single cortical source generating both the N170 and the VPP. Rather, there is certainly a configuration of multiple cortical sources activated simultaneously or within a very short time-frame in many cortical areas, subtending the two sides of the component recorded on the scalp. Simultaneous scalp and intracerebral recordings will have to be performed to disentangle the respective contributions of these sources to the N170/VPP complex.

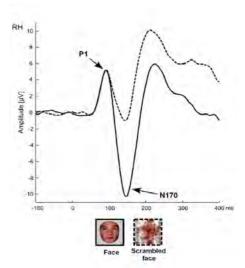


Why should we have a particular interest in this N170 component?

Nowadays, there are hundreds of ERP studies describing the properties of the N170 component in response to faces, and about a hundred studies published every year. Hence, writing a coherent review of this work would be a serious challenge and is probably impossible at this stage (we have written a few reviews, focusing on specific issues: Rossion & Jacques, 2008: specificity; Rossion & Jacques, 2011: mainly on sensitivity to individual faces of the N170; Rossion, 2014: a short review of more recent work).

So why is there so much interest in this component? The first reason for being interested in this component is that the N170 is clearly related to the kind of information that leads to **conscious perception** of a visual stimulus as a **face**. Let's say that you present a visual stimulus that has the same amplitude spectrum as a face but that does not look like a face because the phase of the spectrum is randomized. That is, this phase-scrambled face stimulus has the same low-level visual properties as a face. Yet, it is not *perceived* as a face.

As you can see on the figure on the right (adapted from Rossion & Caharel, 2011), for such a phase-scrambled face, the N170 remains of small amplitude, almost non-existent. This is not true for other visual components. In particular, it is not true for the preceding P1 (peaking at about 100 ms): the P1 is of equal amplitude (and latency) to a face and a phase-scrambled face (it might even be slightly larger for the phase-scrambled image) (Rousselet et al., 2005; 2007; Rossion & Caharel, 2011).



Hence, when it comes to visual perception, the P1 and the subsequent N170 present with fundamentally different response properties. While the P1 is driven by the low level visual properties of the stimulus, irrespective of the meaning of the stimulus for the human brain, the N170 is associated with the information that leads to conscious perception of the stimulus as a face. In writing this, I do not mean that *conscious* perception takes place already at the level (onset) of the N170. Maybe, maybe not. However, what I mean is that the N170 amplitude is related to the kind of information that leads to the conscious interpretation (perception) of the stimulus as a face.

Over recent years, several ERP studies have supported this view, presenting brief face stimuli masked by noise and correlating the ERP signal with conscious reports of seeing a face (e.g., Navajas et al., 2013; Philiastides & Sadja, 2006; Harris et al., 2011; Hansen et al., 2010; Rodriguez et al., 2012). One study has claimed to report N170 responses in the absence of conscious reports of faces (e.g., Suzuki & Noguchi 2013), but the component ("N1a") is not right lateralized anymore, and larger on occipital medial sites than occipito-temporal sites, so that it's difficut to associate with a N170.

Another illustration of the relationship between the N170 and the perception of the stimulus as a face is provided by the N170 recorded to Arcimboldo/Mooney face stimuli. Here the images to compare are the same when they are presented upside-down. However, the perception of the face is altered. Accordingly, the N170 is much smaller in amplitude for inverted Mooney or Arcimboldo stimuli than when the stimuli are presented at upright orientation (George et al., 2005; Caharel et al., 2013).

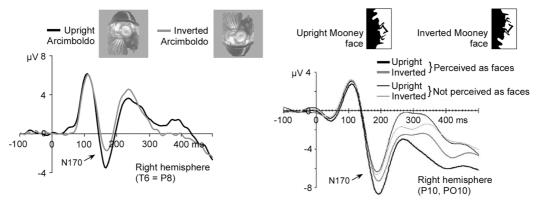


Figure taken from Rossion & Jacques, 2011; courtesy of S. Caharel and N. George, respectively.

Note that if a face photograph is presented upside-down, the N170 is *not* reduced, and is in fact, paradoxically, increased (Rossion et al., 1999), as discussed below. However, there is no contradiction with the findings reported above: when a full face photograph is presented upside-down, it is still perceived as a face.

In the same vein, objects consciously interpreted as face-like ("pareidolia") increase the N170 (Hadjikhani et al., 2009). However, the N170 is *not* increased for stimuli that are similar to faces according to a computational model until humans interpret these stimuli as faces (Moulson et al., 2009). Strikingly, a pair of shapes elicits an N170 only after observers have been primed to interpret these shapes as schematic eyes (Bentin et al., 2002). Most recently, it has been shown that the character combination ":-)", known as an emoticon and used to indicate a smiling face in digital communication, elicits a conspicuous N170 that is substantially reduced if the exact same stimulus is reversed ("(-:"), and thus not interpreted as a face (Churches et al., 2014).

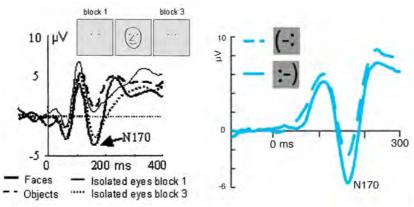


Figure adapted from Bentin et al., 2002; Churches et al., 2014.

As I argued in a recent review, these observations indicate that the N170 is a correlate of the *interpretation* of a visual stimulus as a face: this electrophysiological activity is not only a brain "response" but necessarily involves perceptual knowledge derived from experience of what is a face, incorporating both "bottom-up" and "top-down" processes (Rossion, 2014).

So the answer to the question of why we should we have a particular interest in this N170 component is quite straightforward: since the N170 is the first (in time) component associated with face *perception*, it is a component that is of particular interest for researchers interested in understanding the time-course and the nature of face perception.

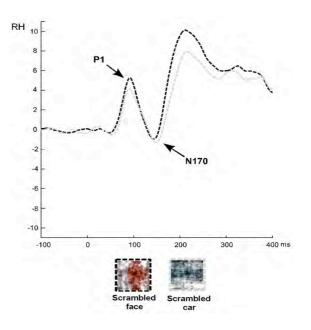
That said, pictures of other objects also elicit a N170 component. No doubt about that. Some objects elicit a larger N170 than others (cars for instance, see Rossion et al., 2000; see also the excellent paper of Schendan et al., 2013, complementing Ganis et al., 2012, and showing the N170 amplitude for faces and a variety of nonface objects across subjects). However, the N170 has a distinct signature for faces: it is typically larger in amplitude for faces than objects. It peaks sometimes earlier also. It shows a clear right lateralization. And it is typically the largest at lateral occipito-temporal sites rather than more medial, occipito-parietal sites. Admittedly, these differences are difficult to quantify objectively, and vary from study to study.

## Does the P1 also reflect face perception? What does sensitivity to faces mean at the level of the P1?

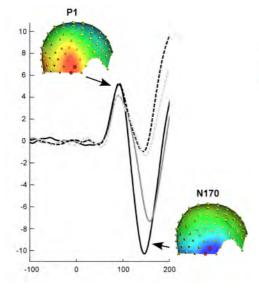
The P1 (or M1 in MEG), which peaks earlier than the N170, has also frequently been associated with face processing. In particular, several studies have reported differential P1 to faces and nonface stimuli (e.g., Halgren et al., 1999; Itier & Taylor, 2004; Liu et al., 2002). However, this observation has often be overinterpreted as evidence for an early stage of face detection, either of "holistic face perception" or "perception of facial parts".

In reality, the P1 sensitivity to faces appears to be driven entirely by low-level visual cues, in particular the differential power spectra of face and other stimuli (Tanskanen et al., 2005). If faces and objects are controlled for low-level visual cues such as differences in power spectrum, there is no difference between faces and objects at the level of the P1, contrary to the N170 (Rousselet et al., 2005; 2007; Ganis et al., 2012).

More strikingly perhaps, we showed that the "P1 face effect" was equally large for phase-scrambled stimuli: phase-scrambled pictures of faces lead to a larger P1 than face-scrambled pictures of objects (here cars; see Rossion & Caharel, 2011).



It means that if you compare the response properties of the P1 and N170 for faces and a highly familiar object category such as cars, you may end up with a clear dissociation between face-sensitivity at the level of the P1 and N170: P1 is accounted for by low-level visual cues, the N170 is not related to such low-level visual cues: its amplitude varies with the percept. **The distinction between the two components therefore marks a border between low-level and high-level vision.** 





The first 200 ms (Rossion & Caharel, 2011). The P1 is larger for both faces and phase-scrambled faces than cars and phase-scrambled cars. Its face-sensitivity is therefore not directly related to the perception of a face per se. In contrast, the N170 is larger (and earlier) for faces than cars, but this amplitude difference cannot be accounted for by low-level visual properties.

# Isn't the N170 peaking too late to reflect the first perception of the stimulus as a face, or the earliest activation of a high-level face representation in the human brain?

I often hear colleagues saying this, but I think it is a misconception. First, the most important thing to consider is that the onset of the N170 is at about 120-130 ms on average (with a great deal of variation across different brains).

In the monkey brain, neurons recorded in the infero-temporal cortex have a mean onset latency of about 90-100 ms in response to faces (e.g., Afraz et al., 2006; Kiani et al., 2005; Tsao et al., 2006). The onset latency of face-selective cells in the human brain is unknown, but comparatively, in the bigger and slower human brain, it is reasonable to consider that it could be 20-30 ms later.

Considering such latencies, and despite all the uncertainty of making relationships between the timing of spike responses and a field potential recorded on the scalp, an onset of 120-130 ms for the earliest activation of face representations in the human brain is not unreasonable. It is fact perfectly compatible with other measures.

Let's say that (high-level) face-selectivity emerges shortly *after* 100 ms in the human brain (this is also what is observed in human intracerebral recordings, Liu, Agam et al., 2009). And of course, there is no definite answer to this quesiton, since it depends on the stimuli that are compared.

Of course, one can observe earlier responses to faces, even by humans. For instance, Crouzet, Kirchner and Thorpe (2010) found saccades towards faces in visual scenes as early as 110 ms. However, it is likely that the earliest saccades towards faces are driven by low-level cues such as a differential amplitude spectra for faces and other visual stimuli (see Crouzet & Thorpe, 2011). The P1 effects showed above indicate indeed that such low-level visual properties can play a role in the early responses to faces. However, at that time, the stimulus is not yet *perceived* as a face by the system.

#### Should we systematically equalize our stimuli for low-level visual cues?

The discussion above may have led to the impression that when we compare faces to other visual stimuli, we need to systematically control for low-level visual cues. Apart from rare cases such as in the paper described above for power spectra and color (Rossion & Caharel, 2011), controlling generally means *eliminating* these cues. Indeed, some researchers use faces and objects that are equalized in luminance, contrast (according to one definition of contrast, generally the Michelson contrast) and even power spectrum (energy per spatial frequency band) (e.g., Rousselet et al., 2005).

Such a procedure can be very important to make a point in a given study. For instance, in order to demonstrate that the larger N170 amplitude to faces than objects is not due to low-level visual cues. This is fine.

However, the stimuli transformed can then become very artificial, very far from the kind of face stimuli that we are exposed to in real life. Since it is difficult to normalize across all color channels, these stimuli are usually presented without color information for instance. Therefore, such transformations remove diagnostic low-level cues for distinguishing faces and objects, but also high-level cues (our brain "knows" that a face

of a certain population is of a specific color as compared to another object category, and this is certainly part of what helps us categorizing faces).

In some studies, the "luminance-contrast-power spectrum-color normalized" face stimuli are even of the exact same size, with all features realigned (e.g., Rousselet et al., 2008, faces vs. houses).

My view on this issue is that an obsession with the control kills many interesting phenomena, and I would strongly advice researchers in this area to be careful in wanting to control for everything (and forcing others to do so !). There needs to be a fine balance between control of low-level visual cues in a given study and keeping in the stimuli all the cues that are important to understand the phenomenon that one is interested in. We have discussed these issues in several papers (Rossion & Jacques, 2008; Rossion & Caharel, 2011; Rossion, 2014, box #1) but I'd like to write a few more words here on that.

For instance, since overall *luminance* will depend on the conditions under which the picture is taken, and these can vary greatly between the different pictures across categories, it makes sense to equalize overall luminance between the set of faces and objects compared.

It is already less obvious to me for *global contrast*. Faces are highly contrasted stimuli for instance, with some regions of a face being dark (eyebrows, dark eyes) and others being very light (cheeks, forefront). In a way, this is a property that could also be part of what makes faces different kinds of stimuli than some other object categories. Contrast within the stimulus is a cue that can be picked up by the system to categorize faces *vs.* objects, and discriminate different faces.

Power spectrum is another one. Different object categories differ in their power spectra. In particular, faces have even more energy in low-spatial frequency bands than other object categories (Keil, 2008). If we systematically equalize for power spectra across categories, for instance by using for all stimuli the average of the amplitude spectra of all face and non-face stimuli of a given set, we remove an interesting aspect of what defines a face also for the visual system.

Again, once it has been done in a given study and it has been shown that the larger N170 in response to faces than other object categories is not explained by such cues, it's fine. However, in subsequent studies, one does not necessarily need to remove these cues in a study that targets the N170 to manipulate task or stimuli variations within the face domain for instance. That is, when one compares a set of faces to another set of faces, or the same faces across task manipulations. Faces vary in terms of contrast and spatial frequency also, in terms of diagnostic color cues, etc ... Removing such cues removes part of the phenomenon we are interested to study.

The best example comes from studies that investigate the "other-race" face effect: on top of equalizing power spectrum and contrast, some of these studies remove color from the faces! This does not make sense to me. Color is an essential part of what defines faces of different human populations of the world. It is a highly interesting cue, and removing color in such studies does not make sense: it removes a substantial part of the phenomenon we are interested in.

In general, my feeling is that the problems with studies of the N170 component have not been so much due to a lack of absolute control of low-level visual cues. It has been the case for the visual P1 though, a component that is highly sensitive to luminance, contrast, power spectra variations, .... And, of course, given that the N170 immediately follows the P1, any effect on the P1 could be simply propagated to amplified at the N170 level. This why in any N170 study, interpretation of the data must be made with great care. And peak-to-peak measures with respect to the P1 should also (not exclusively) be considered when dealing with the N170. Regarding this last point, while time-point statistical analyses, ignoring the components, have been proposed as a solution to this issue, I think that they will complement but will never replace fully an ERP component based approach. As we just saw, the P1/N170 border appears to mark a categorical border between low-level and high-level vision.

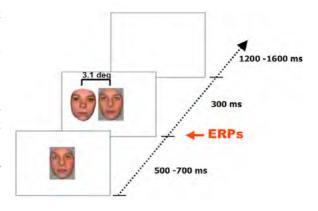
## Now that we have a better idea of what the N170 marks, what we can we do with it?

In general, I have had little interest in trying to define the N170 as a "stage" of face processing. The N170 reflects in fact a fairly long time window (130-200 ms). During this time-window, there are certainly many visual areas activated, in particular in the ventral visual stream. Associating the N170 to a "stage" of processing and a specific cortical source does not seem plausible to me. Rather, it is likely that there are many sources and many processes interlocked in time that takes place during the N170 time-window.

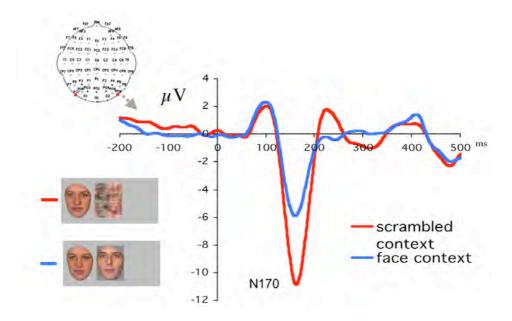
However, since the N170 time-window is associated with the beginning of high-level visual processes, one can use the N170 as a "tool" to define these processes and understand the nature of the perceptual encoding of faces. This is the research program that we have attempted to pursue over the past 15 years, and which is illustrated below.

#### N170 and visual competition

In a very simple study, we found that when observers fixate a central face stimulus remaining on the screen, the N170 response to a subsequent face stimulus presented at a different location is substantially reduced (with respect to a control condition in which the first stimulus is a phase-scrambled face) (Jacques & Rossion, 2004). Importantly, the first stimulus remains on the screen when the second appears.



Note that this reduction is also found when you present first two lateral face stimuli, side by side, outside of fixation: the N170 elicited by a third face stimulus appearing at fixation is largely reduced (compared to a situation when two phase-scrambled stimuli are presented initially) (Jacques & Rossion, 2006). However, the N170 is reduced to a lesser extent for a central target than a lateral target face (Jacques & Rossion, 2006).

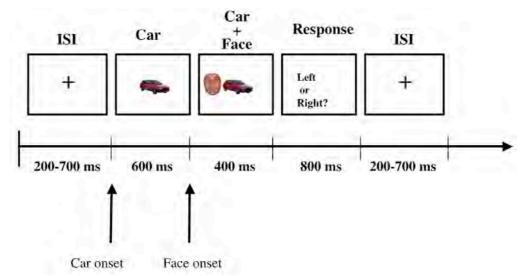


These observations are in line with single-cell recording studies in the monkey infero-temporal cortex showing that neurons tuned to respond to face stimuli exhibit a decrease of their response when more than one stimulus is present in the visual field (e.g. Miller et al., 1993). These effects are generally interpreted as reflecting a competition between visual stimuli for neural representation, to the extent that these stimuli recruit a common population of neurons (Desimone, 1998; Keysers & Perrett, 2002). Thus, the observation of a reduced N170 when 2 face stimuli are presented next to each other suggest that individual faces compete for neural representation at this latency.

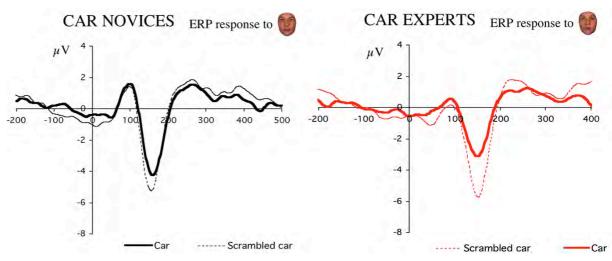
At first glance, these effects are not that exciting: it makes sense that if the system is busy processing a face, the presentation of another face cannot elicit an additional (large) increase of activation. However, it shows at least that the initial representation of faces as tagged by the N170 has a large receptive field (otherwise the competition would take place at a later stage). Most importantly, it provides us with a nice tool to study the competition between faces and other visual stimuli. This is what we did in a series of studies described below.

#### N170 and visual expertise

A major interest of the concurrent stimulation paradigm in scalp ERPs is that it can be used as a tool to test the extent and the time course of the interaction between different shape representations. In two ERP experiments, one with Chun-Chia Kung and Michael Tarr, and the other one with Tim Curran, we showed that fixating non-face objects in a domain of expertise, novel objects (asymmetric Greebles) or cars, leads to a reduction of the N170 elicited by faces presented next to the central object (Rossion et al., 2004; Rossion et al., 2007, respectively). These observations suggest that when presented concurrently, faces and non-face objects in a domain of expertise compete for early visual categorization processes in the occipito-temporal cortex.

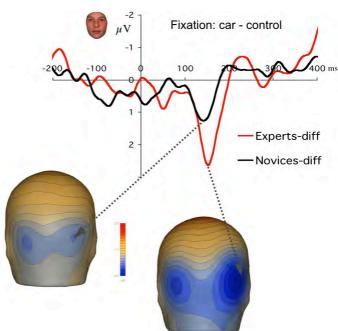


Our study was not the first (and last) to test for such competition effects between faces and visual objects of expertise.

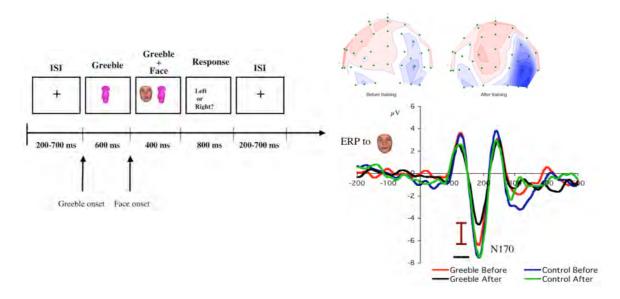


However, a particular interest of our expertise studies is that the effects are very large and clear, obtained in a very simple paradigm, and yet specific in terms of their spatio-temporal localization (N170, right occipito-temporal hemisphere).

Moreover, the sensory competition effects are significantly correlated with the amount of visual expertise of the participants (see Rossion et al., 2007).



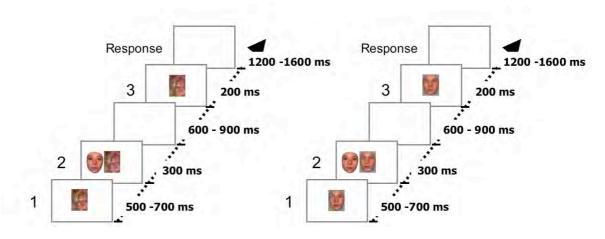
And, it is replicable and very similar in different studies (see Rossion et al., 2004; 2007).



Following this work, we used the concurrent stimulation paradigm to test the respective role of *spatial attention* and *sensory competition* in accounting for the amplitude reduction of the N170 during dual face stimulation (Jacques & Rossion, 2007). In that study, ERPs time-locked to a lateralized face stimulus were recorded while subjects fixated either a face or a scrambled face stimulus (stimulus factor), and were engaged in either a high or a low attentional load task at fixation (task factor).

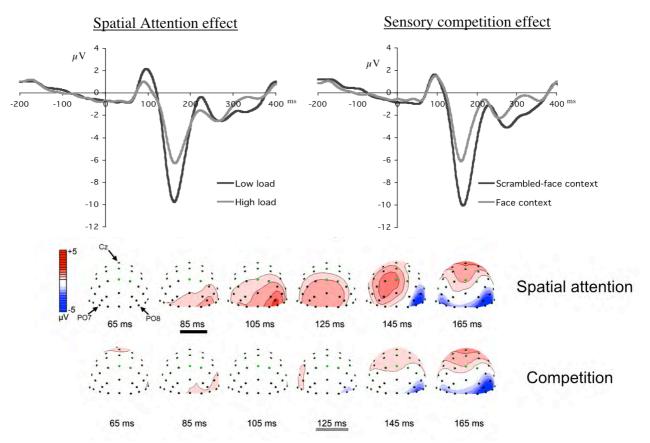
A. Low attentional load at fixation = judge the side of the lateralized face

# B. High attentional load at fixation = match the luminance of the first and third stimuli (central stimuli)



In these conditions, the N170 amplitude to the lateralized face stimulus is reduced both when the central stimulus is a face and when the attentional load at fixation is high. However these effects of stimulus and task factors on the N170 amplitude are largely **additive**. Most importantly, spatial attention modulates visual processes as early as 80

ms after stimulus onset, whereas sensory competition effects starts at the onset of the N170, at about 130 ms.



These results provide clear evidence that (1) the N170 in response to faces can be strongly modulated by spatial attention and (2) sensory competition between face representations in the extrastriate cortex reflects distinct neural processes than spatial attention.

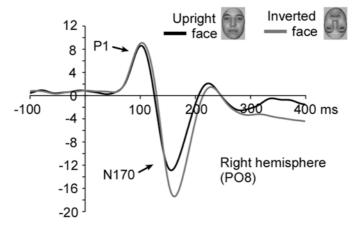
It is a quite important demonstration also because the effects of expertise described above could have been attributed to attention (i.e., experts paying more attention to cars for instance, so reducing the response to the lateralized faces). This is the kind of "easy" arguments that are usually used to dismiss visual expertise effects (when one is short of arguments, there is always the attention account to use ③). Although there a number of (good) reasons to believe that attention could not account for the competition effects mediated by expertise, the study in which attention was manipulated shows that if experts paid more attention to cars than novices then there should have had a P1 reduced relative to novices in the 2 expertise studies (Rossion et al., 2004; 2007). It was not the case.

#### Face inversion and the N170

In his early studies, Jeffreys (1993) found a delay of latency of the VPP for inverted faces. In one experiment, Bentin et al. (1996) also reported a significant latency delay for inverted faces, and also mentioned a small increase of amplitude. Since then, the peak latency delay of the N170 for inverted faces has been reported in many studies, including a number of studies performed in the face categorization lab. This latency

delay is compatible with the delay of response latency found for inverted faces in faceselective cells of the monkey brain.

However, what is really surprising is that the N170 is generally increased in amplitude for inverted faces, as in the example below. Besides the short report of Linkenkaer-Hansen et al. (1998), I believe that we reported the first clear evidence of this amplitude increase to inverted faces (Rossion et al., 1999).



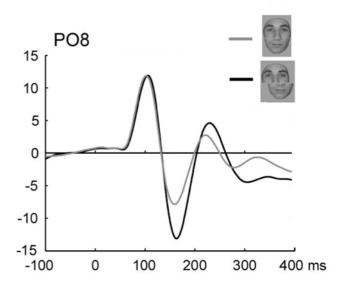
If I am not mistaken, we were also the first to show that this paradoxical increase of amplitude and latency only holds for faces (at least when we compared to a series of nonface mono-oriented objects) (Rossion et al., 2000).

In the 1999 paper, we used faces only, and we also proposed two possible accounts for this paradoxical increase:

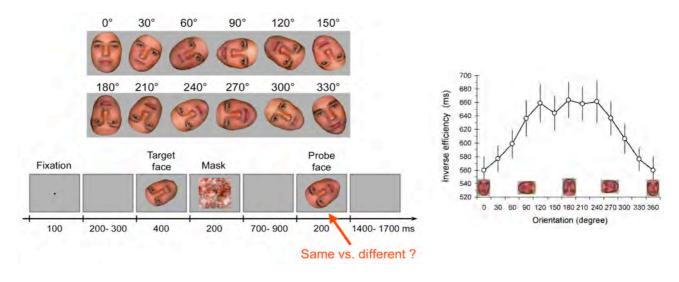
- (1) the loss of configural/holistic encoding following inversion could have resulted in an *increase of difficulty* for encoding the face stimulus, leading to a larger and delayed face encoding process.
- (2) that the larger amplitude observed for inverted faces might be a result of the recruitment of additional processing resources in object perception systems.

Although other authors (mainly Roxane Itier) have proposed different - plausible - accounts of this effect, I still believe that these two possibilities, which could be complementary, account for a large part of the effect. Indeed, other transformations that are well-known to disrupt holistic/configural face processing lead to the same effect.

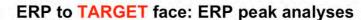
For instance, if you cut the face in two parts, as in the control condition of the composite face effect, you get the same effect as when you invert a face: increase of N170 latency and amplitude. Letourneau & Mitchell (2008) showed that first. More recently, we used a series of control stimuli to show that this increase cannot be accounted for by a general effect of spatial misalignment of visual patterns (Jacques & Rossion, 2010).

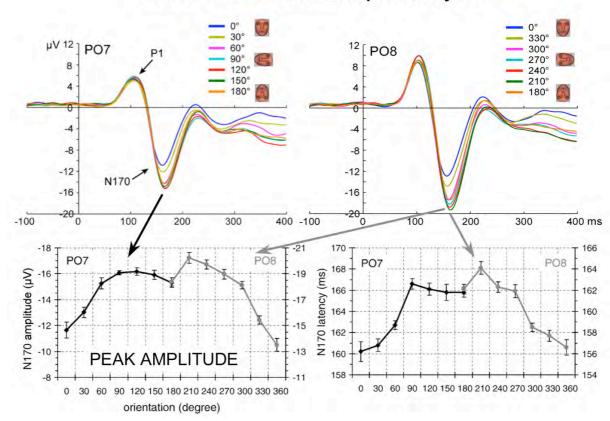


I am also convinced that the effect of inversion on the N170 is not an epiphenomenon. Rather, it seems to reflect something functional, such as a loss of holistic/configural face encoding. Again with Corentin Jacques, we presented face stimuli at 12 orientations, from 0° to 330°. We used a delayed matching task and measured performance on the second face.



In that study we showed that the amplitude of the N170 varies according to a "M-shaped" function, just like behavior (Jacques & Rossion, 2007).





What about the account of an amplitude increase for inverted faces explained by recruitment of resources from a more general object processing system? There is evidence indeed from several fMRI studies that non-face-selective lateral occipital cortex activation is enhanced in response to inverted faces (e.g., Haxby et al., 1999). However, there is no such amplitude increase of inverted faces in the middle fusiform gyrus, in the so-called fusiform face area (FFA), but rather a small decrease. I also recommend having a look at the paper of Rosburg and colleagues (2010) with intracranial recordings: these authors found an increase of amplitude to inverted faces in the lateral occipital cortex but not in the ventral temporal cortex.

So all in all, I'd like to write two more things about this increase of amplitude following inversion of the face stimulus:

First, the increase of amplitude is observed only when inversion does not prevent the *interpretation* of the stimulus as a face, as when clear photographs of faces are used. That is, if you invert Mooney faces, they are not seen as faces anymore, and so you observe a large *reduction* of the N170. It is important that the two phenomena are not confounded: the *increase* is observed when the stimulus can still be perceived as a face.

*Second*, one should not confound this increase of amplitude with the face inversion effect on the N170: the fact that repeating the same face identity leads to a decrease of amplitude on the N170 for upright but not for inverted faces (Jacques et al., 2007, see below).

#### **Development**

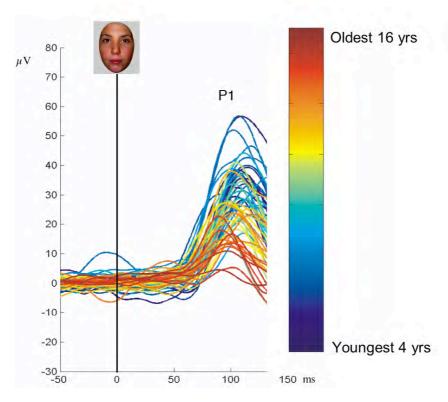
How does the N170 evolve across development? This is an important issue because face recognition performance appears to improve a lot with age, at least until adulthood (Carey, 1992). Yet, authors are divided with respect to the explanation of this phenomenon, in particular whether it reflects the maturation of face-specific or general processes.

This is where the study of the N170 can be important. When you measure behavior of a child at a face recognition task, it could be that face perception is as mature as in adulthood but that performance is less good because of other factors in development that will influence the behavioral response (attention, understanding of the task, motivation, selection of responses, ...). However, since the N170 reflects the early activation of perceptual face representations, one can measure how perception of faces varies across developments in a behavior-free measure.

In a series of studies, Itier, Taylor and colleagues showed that the N170 undergoes dramatic changes across development, from 5 years old until adulthood: linear reduction of latency and large changes of amplitude. However, it remained unclear whether these modifications were specific to faces.

With a postdoc in my lab, Dana Kuefner, we performed an ERP study in children and adolescents (4 to 18 years old) in which we compared the N170 to pictures of faces, cars and their phase-scrambled versions.

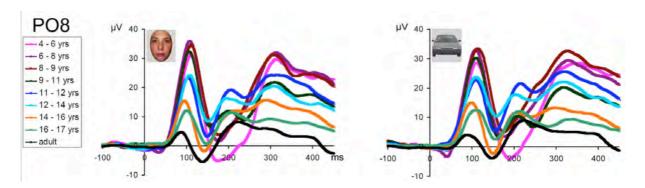
We found that there are indeed major changes in the basic response properties of these components (reduction of latency and amplitude, lateralization of posterior topography), in particular the P1, which decreases dramatically with age (as described previously in other studies also with non face stimuli)



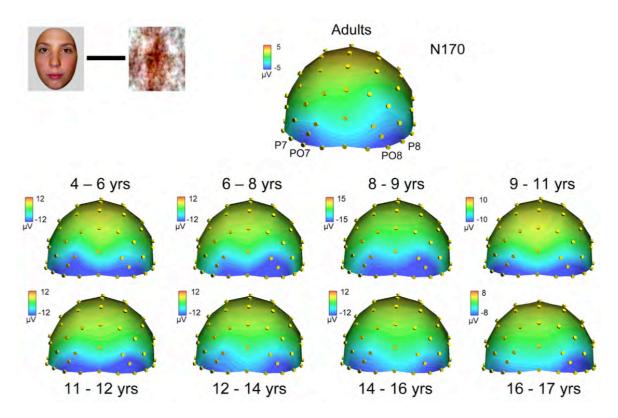
However, these changes are found for any kind of visual stimulus for the P1. And,

they are found for both faces and objects (cars) for the N170 (Kuefner et al., 2010). A larger N170 for faces than cars, with a right lateralization, is found in younger children and does not appear to increase with age.

In short, contrary to what was claimed in previous studies, we found *that the P1 and N170* do **not** change specifically for faces between 4 years of age and adulthood.



We concluded that there is no evidence (so far) from the characteristics of the N170 that the perception of faces changes across development.



However, it does not mean that perception of faces does not change with age. For instance, response properties of the N170, such as its sensitivity to individual faces, may well change across development. In fact, such an observation would be more compatible with what is known from behavioral studies: what truly changes during development is the performance at individualizing faces, not really at detecting faces. There is a long way before testing that in children, and what we'll first have a look at is the sensitivity of the N170 to individual faces in adulthood. This has been a major area

of interest in my laboratory over the past few years in adults, and I'd like to show you a summary of that work here.

#### Evidence for individualization of faces as early as the N170

As I mentioned earlier, when one refers to the N170, it is in fact a quite a long window of duration because it ranges between about 130 ms and 200 ms (with a substantial amount of variation between people in terms of peak latency). While the N170 can be considered as a marker of the activation of a generic face representation, we believe that there is much more concerning face processing that takes place during the N170 time-window.

Interestingly, a number of authors including Shlomo Bentin and Martin Eimer have associated the N170 with the structural encoding stage of the Bruce & Young (1986)' information processing model of face processing. While I do not subscribe to the idea of associating a component with a stage of processing, I often point out that "the structural encoding stage" is NOT a face detection stage in the Bruce & Young (1986) model. It was conceptualized by the authors as a level "which capture those aspects of the structure of a face essential to distinguish it from other faces" (Bruce & Young, 1986, p. 307).

Therefore, if the N170 corresponds to the structural encoding stage of that model, then it must reflect within-category discrimination! (= individualization of faces).

Most importantly, recordings of single neurons in the monkey infero-temporal cortex show that as early as these cells start to discharge selectively to faces (about 100 ms, see above), information about individual faces start to accumulate (i.e., different cells respond at a different rate to different faces, e.g., Rolls & Deco, 2000).

Considering this, it would make complete sense that beyond face/object discrimination, individual faces can be discriminated already during the N170 time-window. I believe that there is now sufficient evidence that this is the case, and although others have provided evidence supporting this view, it has been one of the main focus of interest for the research carried out in my lab over the past few years. We developed two paradigms to test that.

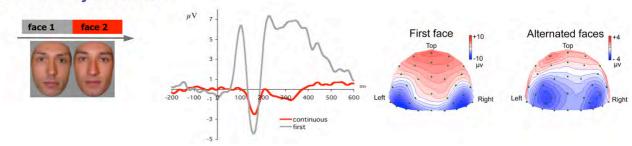
First, we realized that all ERP studies of face perception used versions of the "flash VEP" paradigm: a complex and highly salient face stimulus is flashed at once to the system, leading to a series of ERP responses that needs to be interpreted.

With Corentin Jacques, we developed a new paradigm that would be the equivalent of the "pattern reversal VEP" with faces: a train of 2 faces alternate with each other at about 1.3Hz (random duration between 500ms and 700ms). In such a "face identity reversal" paradigm, the changes of low-level visual information from face A to face B is limited (and was manipulated by morphing in that experiment). What is changing is the difference between the two individual faces, that is, facial identity.



The results were quite interesting: when we averaged all the pieces of EEG that followed a reversal of identity, we found that the P1 component was virtually absent: the waveform was flat until 100 ms and then there was a negative deflection peaking exactly at the latency of the classical N170 component! It topography was also remarkably similar to the whole N170 component (Jacques & Rossion 2006).

#### « face identity reversal »

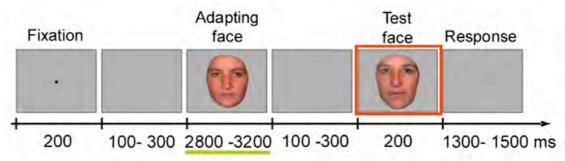


To us, this result indicated that if one restricts the change in the stimulus to the properties that characterize an individual face, it is sufficient to elicit a N170-like component. We also showed in that study that the response was larger for a change of identity that was perceived as larger than another change, even though physical differences between the 2 switches of identity were kept constant ("categorical perception", see Jacques & Rossion 2006).

The paradigm is quite powerful because you could get a lot of trials in a very short time. However, its range of application is also limited because you need to use very similar faces and minimize motion onset between pictures.

This is why, over recent years, we have rather concentrated on using a *face-identity* adaptation paradigm in ERPs to understand the nature and dynamics of coding for individualizing faces.

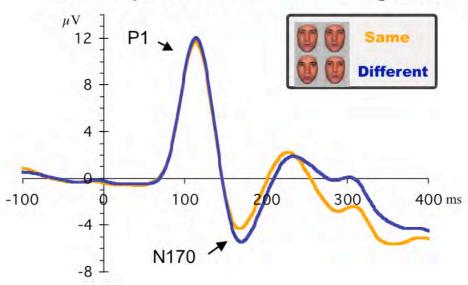
To start, we observed that a number of studies failed to report any face identity repetition effects on the N170, or observed very weak effects, so that a number of authors considered that individual face discrimination was not taking place at that latency. Therefore, inspired by a study of Gyula Kovács and colleagues (2005) and by behavioral studies of face adaptation, we used a paradigm in which we maximized our chances to observe something by presenting a first face stimulus for several seconds followed after a very brief duration by a second face stimulus (Jacques, d'Arripe & Rossion, 2007).



This second face could be either the same identity, or another identity (all unfamiliar faces). Importantly, we changed the size between the adapter and target face, and we also used different pictures of the same individual in the condition when the same face was repeated. This way, we minimized low-level repetition effects.

In these conditions, what you get is a **reduction of the N170 amplitude** when the target face is the same person as the adapter face. The effect is not big, but it can be more than 1 microvolt in that study and highly significant at the group level. There are differences taking place later, but it is the earliest effect (if low-level adaptation is minimized for instance by changing size between the adapter and the target face).

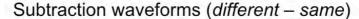
## ERP response to TEST face - Right hemisphere (PO8)

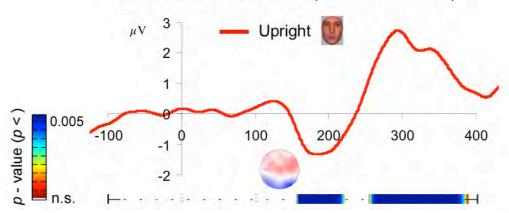


This observation shows clearly that at least as early as the N170 peak (about 160 ms following stimulus onset), the system has accumulated sufficient evidence to individualize faces.

It is true that some studies do not find a significant difference at the level of the N170, using different stimulation parameters. However, these are null results, and I think that there are enough positive results of this sort now in the literature to make the point that individual faces are coded as early as the N170 time-window.

Moreover, again, the topographical map of this difference show the typical occipitotemporal right lateralization.

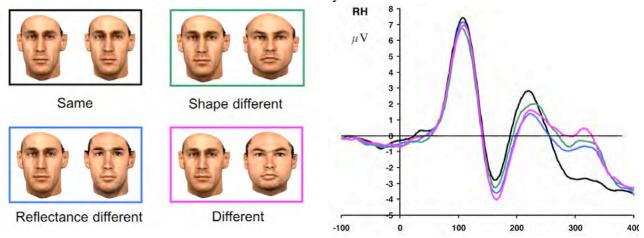




Now that we know that individual faces are coded as early as the N170, what can we do?

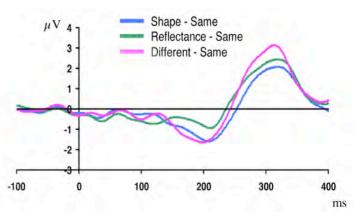
Well, let's play with that effect!

In one study that I like very much, we tried to determine what kind of information from the face conveys most of the effect. We used the identity-adaptation paradigm with faces that vary either in 3D shape or in 2D surface reflectance (color and texture), the two main sources of information for facial identity.



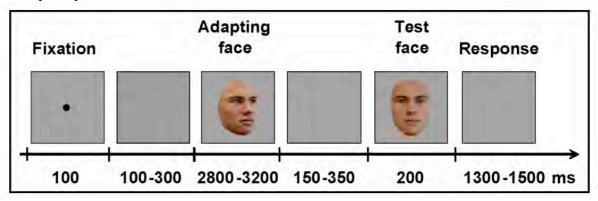
Behaviorally, we replicated previous findings: people are as accurate and as fast to discriminate individual faces based on shape or surface reflectance (e.g., O'Toole et al., 1999). When you have the two kinds of information added, people perform even better. This is also what we found at about 300 ms following stimulus onset: the difference between the condition in which the two sources of information differed ("different") showed the largest difference with the condition in which the same face image was repeated (Caharel, Jiang et al., 2009).

However, and most importantly, at the level of the N170, we found that a difference in 3D shape alone led to a significant difference, while 2D surface reflectance alone was not sufficient to elicit such a difference. The effect for 3D shape alone was as large as the effect observed for the addition of the 2 sources of information.

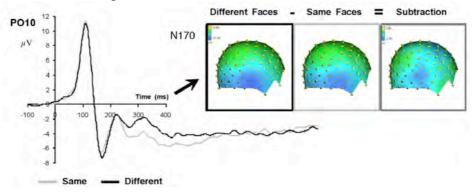


This finding supports the view that individualization of the face is based on both kinds of sources of information but that information about shape is accumulated earlier than information about color and texture (Caharel, Jiang et al., 2009). This observation highlights a great advantage of ERPs over behavioral studies in this area of research: with ERPs we disclosed a difference in the timing of processes that behavioral results could not reveal.

Next, we investigated whether this face identity adaptation effect could be observed across head view changes. Again, since face-selective neurons in the monkey inferotemporal cortex show viewpoint-tuning in the form of a bell shape function, we reasoned that if an angle smaller than a 3/4 profile was used, we should still get an identity-adaptation effect.



In this latter study (Caharel et al., 2009), we found indeed that the N170 (only in the right hemisphere) was smaller in amplitude when the same facial identity was repeated immediately after an adapter face, even with a substantial amount of viewpoint difference (30° depth rotation).

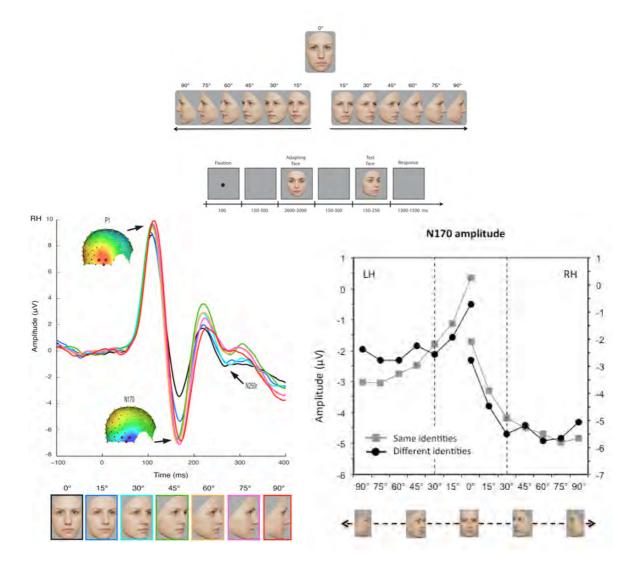


Be careful though: this result is sometimes erroneously taken as evidence for viewpoint-invariant face representations at the level of the N170. It's not. First, we did not really test viewpoint-tuning, but sensitivity to adaptation across viewpoints. Second, our results show that the tuning to viewpoint for a certain identity is not sharp, that's all. If the representation is viewpoint-dependent but that there is a bell shaped function, then there could still be an effect of identity-adaptation across a 30° change, that would disappears completely at a 3/4 profile (45°).

In fact, in our most recent work, that's exactly what we have tested (Caharel et al., 2015): we adapted to a full front face and then we presented faces under 6 possible viewpoints, with a change of identity or not. We found two results:

- 1. The N170 adapts to viewpoint (independently of identity) for a 0° change and less so to a 15° change. Then there is no adaptation.
- 2. Adaptation to identity (i.e. difference between same and different faces repeated) resists until 30° viewpoint change.

The first observation shows that a face is encoded in a view-dependent manner, being matched to either a full-front or a profile face view: a 15° view lies in between. The second one shows that individual face representations activated as early as the peak of the N170 generalize partially across views (up to 30°).



I also want to mention again that the fact that another study can fail to find an identity adaptation effect on the N170 in such a paradigm (with small changes of head rotation) cannot rule out the positive result that we observed here in several studies): one has indeed to use the most sensitive paradigm as possible, given that these effects on the N170 are not big. Some of my colleagues have also toned down the interest of the N170 adaptation effect across viewpoints because it is much smaller than the late difference (that can be indeed observed on the figure from the study of Caharel et al., 2009). For my part, I am interested in the N170 modulation because it's the first one in time, and I know that at this point the system has accumulated sufficient evidence to show a sensitivity to individual faces, even across head views. Of course, evidence goes on to accumulate in the processing of the face, but I don't know if such late effects have much to do specifically with face perception.

One thing that surprised us though is that instead of increasing, the N170 identity adaptation effect across head rotation disappeared when we used **personally familiar faces** (Caharel et al., 2011)! Given that people perform usually better at matching familiar than unfamiliar faces across head rotation, we had expected the opposite. However, we found that with familiar faces, a significant effect appeared on the left hemisphere N170, suggesting that when familiar faces are used, identity-representations can be generalized across views in the left hemisphere. As for the behavioral advantage at matching familiar over unfamiliar faces, we found that it was related to late differences in the ERPs.

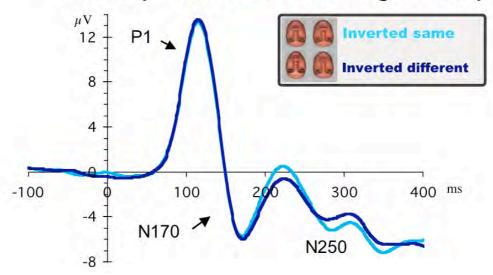
#### Early individualization of faces (N170) is based on a holistic representation

One (very) important theoretical issue in the field of face perception is whether the encoding of the face is first performed part-by-part (one eye, the mouth, ... or fragments) towards a global representation, or if the face is initially encoded as a whole template.

At the level of the encoding of an individual face at least, our face-identity adaptation paradigm suggests that the second view (initial encoding of the whole individual face) is correct.

First, in the study of Jacques et al. (2007) we showed that the identity adaptation effect at the level of the N170 was not found when the exact same faces were presented upside-down, a manipulation that is well know to disrupt holistic processing.

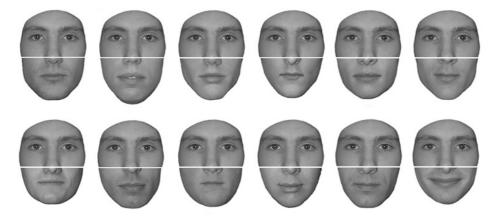
### ERP response to TEST face - Right hemisphere (PO8)



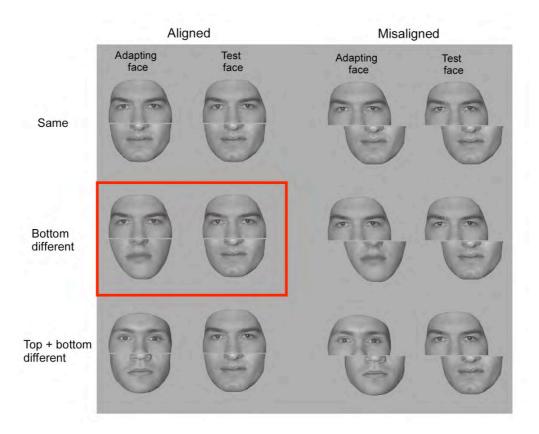
This result strongly suggests that individualization of faces at the level of the N170 at least is based on information whose processing is lost by perception. Since inversion is known to affect greatly holistic/configural encoding of individual faces, it is reasonable to believe that the individualization of faces at the level of the N170 is based on a holistic representation.

#### Can we demonstrate that more directly?

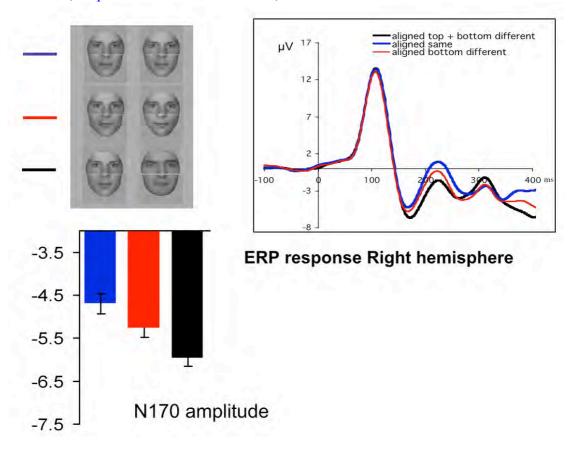
In a study with Corentin Jacques, we used a variation of the composite face paradigm (Young et al., 1987), taking advantage of the visual illusion that such (unfamiliar) composite faces can create (see Rossion, 2013 in Visual Cognition for an extensive review).



This time, we asked participants to focus only on the top half of a face (defined as the half above a tiny white line or gap) and match this top half. The irrelevant bottom half had to be ignored, both for the adapter face and for the target face. When the two top halves were identical between the adapter and target, this bottom half could also be either of the same identity for the adapter and the target, or, of a different identity. In this latter case, a strong visual illusion is elicited: despite being physically identical the two top halves appear dissimilar.



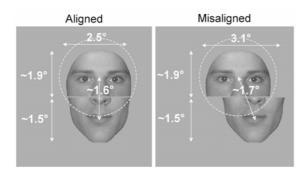
In this condition, we found a larger N170 than when the two top halves appear identical (Jacques, & Rossion, JOV, 2009).



This result thus strongly reinforces the view that the individualization of faces at the level of the N170 is based on a holistic representation.

Note that the increase of amplitude was not large, and certainly not as large as when the two faces were truly physically different (replicating the result observed by Jacques et al., 2007). This makes sense since the perceived dissimilarity between the two faces is not as large as when they are truly physically distinct.

Moreover, and more importantly, we also showed that when the top and bottom halves are very slightly **misaligned**, removing the visual illusion, the N170 identity adaptation effect disappears



Again, we take these results as evidence for an early activation of. It is an important observation because it suggests that an individual face is not encoded part-by-part (or at least that these parts are not interpreted as face-like by the system) but rather as a holistic representation.

These results have also been replicated more recently in another study (only with aligned faces, and with only the top halves changing in the real "different faces" condition) using an oddball paradigm (Kuefner et al., 2010). This latter study demonstrated that these observations can be independent of the decision-related components and behavioral responses in the composite face paradigm.

I guess that's all for now ... see our publications for more in depth discussion of these issues. Although our lab keeps a high interest in this N170 work, our most recent work in human electrophysiology has been with fast periodic visual stimulation (FPVS) to increase objectivity and sensitivity of the approach: see

http://face-categorization-lab.webnode.com/research/steady-state-face-potentials-ssfp-/

#### BIBLIOGRAPHY (lab papers) and main finding(s) of each paper

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

**see also our review chapter:** Rossion, B. & Jacques, C. (2011). **The N170: understanding the time-course of face perception in the human brain**. In *The Oxford Handbook of ERP Components (2011)*, Edited by S. Luck and E. Kappenman. Oxford University Press, 115-142.

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

Rossion, B., Delvenne, J.-F., Debatisse, D., Goffaux, V., Bruyer, R., Crommelinck, M., Guerit, J.-M. (1999). Spatio-temporal brain localization of the face inversion effect. *Biological Psychology*, 50, 173-189.

One of the first study (with the short paper of Linkenkaer-Hansen et al., 1998) to report a significant increase of the N170 in response to inverted faces. In our discussion, we raised two possible accounts for this paradoxical increase: (1) that the loss of configural processing following inversion could have resulted in a selective amplification of neural activity devoted to faces because of an increase of difficulty of processing; or (2) that the larger amplitude observed for inverted faces might be a result of the recruitment of additional processing resources in object perception systems. I still believe that these two possibilities probably account for part of the effect, even though other authors have proposed alternative explanations.

Paper submitted to *Neuroreport* and rejected without option to respond to comments, then submitted to *Biological Psychology*.

Rossion, B., Campanella, S., Gomez, C., Delinte, A., Debatisse, D., Liard, L., Dubois, S., Bruyer, R., Crommelinck, M., Guerit, J.-M. (1999). Task Modulation of Brain Activity Related to Familiar and Unfamiliar Face Processing: an ERP Study. *Clinical Neurophysiology*, 110, 449-462.

One of the first N170 studies comparing the perception of familiar and unfamiliar faces, and failed to find a modulation of the N170 by long-term familiarity of the face.

#### Paper first submitted to Clinical Neurophysiology

Rossion, B., Gauthier, I., Tarr, M.J., Despland, P.-A., Linotte, S., Bruyer, R., Crommelinck, M. (2000). The N170 occipito-temporal component is enhanced and delayed to inverted faces but not to inverted objects: an electrophysiological account of face-specific processes in the human brain, *Neuroreport*, 11, 1-6.

The first study to compare the effect of inversion on the N170 to faces and objects. We replicated the increase of amplitude and latency for inverted faces, and showed that this effect did not hold for pictures of familiar objects: chairs, cars, shoes, houses, or a novel object category (greebles). Therefore, the N170 is not only a component that is larger in response to faces than other objects, but it also shows some specific modulations to the same kind of transformation (inversion). A (smaller) latency increase with inversion was found in a next study for pictures of cars though, and for words (Rossion et al., 2003, Neuroimage).

#### Paper first submitted to Neuroreport

Rossion, B., Gauthier, I., Goffaux, V., Tarr, M.-J., Crommelinck, M. (2002). Expertise training with novel objects leads to face-like electrophysiological responses. *Psychological Science*, 13, 250-257.

This was an ambitious study, in which we wanted to demonstrate that the increase of latency and amplitude of the N170 to faces could be also observed for nonface objects following expertise training. We used Greebles for that.

Admittedly, the effect was not as convincing as we wanted: it concerned only the N170 latency increase following inversion, and the effect was somewhat larger on the left than the right hemisphere. A bit disappointing overall, even though further studies have shown similar effects (e.g., Busey & Vanderkolk, 2005).

#### Paper first submitted to Psychological Science

Rossion, B., Joyce, C.J., Cottrell, G.W., Tarr, M.J. (2003). Early lateralization and orientation tuning for face, word and object processing in the visual cortex. *NeuroImage*, 20, 1609-1624.

Nothing special about that study in my opinion, yet it's one of the papers that gets the most citations! We replicate the N170 latency delay for inverted faces, and show that it is larger than for other mono-oriented stimuli such as cars and words. One interesting observation is that we compare the lateralization of the N170 to faces and words in the same study, showing a clear right/left dissociation. Source localization of faces vs. objects differences were also reported in this paper, suggesting the primary contribution of a ventral ocicpito-temporal source.

#### Paper first submitted to NeuroImage

Goffaux, V., Gauthier, I., Rossion, B. (2003). Spatial scale contribution to early visual differences between face and object processing. *Cognitive Brain Research*, 16, 416-424.

We compared the N170 to pictures of faces and cars presented under normal conditions or spatially filtered (low-pass, high-pass). The N170 face effect (larger amplitude to faces than objects) and the latency delay with inversion disappeared for faces presented with only high-spatial frequency (HSF) information. This study suggests that the early encoding of face-specific representations is supported largely by low-spatial frequency (LSF) information. We controlled for the higher contrast provided in the LSF by combining faces with a mask that was filtered in the opposite frequency range (e.g., LSF face with HSF mask). While this procedure offers a better control than when directly comparing HSF and LSF, one limitation of the study is that the LSF mask (high contrast) might have reduced the visibility of the HSF face, increasing the effect.

#### Paper first submitted to Cognitive Brain Research

Jacques, C. & Rossion, B. (2004). Concurrent processing reveals competition between visual representations of faces. *Neuroreport*, 15, 2417-2421.

Subjects fixate a central face that remains on the screen while the N170 to a lateralized face is recorded. We show that the N170 is strongly reduced in this condition, compared to when subjects fixate a phase-scrambled stimulus. This effect reflects a form of competition between faces, which is initiated at the level of the N170. It provides the platform for studies in which subjects fixate objects of expertise while the N170 to a face is recorded (Rossion et al., 2004, below; 2007 in JOCN).

#### Paper first submitted to Neuroreport

Rossion, B., Kung, C.-C., Tarr, M.J. (2004). Visual expertise with nonface objects leads to competition with the early perceptual processing of faces in the human occipitotemporal cortex. PNAS, 101, 14521-14526.

An observer fixates the picture of a Greeble in the center, and the subsequent appearance of a face on the right or left of the Greeble (which remains there) leads to a N170. However, this N170 is largely reduced in amplitude if the observer has been trained with (other) Greebles as compared to the N170 before training, particularly in the right hemisphere. Training does not affect the N170 amplitude when participants fixate a control stimulus. This result suggests that the perceptual encoding of the face suffers from the visual competition created by the fixation of the Greeble stimulus. Irrespective of your interpretation of these findings (and attention is not a valid candidate, see Jacques & Rossion, 2007, Cerebral Cortex), while studies on visual expertise have been criticized for the small and non-replicable effects that they often report, this one truly reports a big effect, in a simple paradigm.

#### Paper first submitted to PNAS

Joyce, C.A.& Rossion, B. (2005). The face-sensitive N170 and VPP components manifest the same brain processes: The effect of reference electrode site. *Clinical Neurophysiology*, 116, 2613-2631.

The N170 is systematically associated with a larger positive potential on the vertex, the vertex positive potential as described by Jeffreys in early studies (1989). In these early studies, the reference electrode was usually a mastoid channel, which emphasized the vertex positive potential and minimized the occipito-temporal negativity that was later termed the N170 by Bentin et al. (1996). Here we compared the N170 under several reference electrode configurations (mastoids, nose, earlobes, non-cephalic, common average) to show that the VPP and N170 are indeed two faces of the same dipolar configuration: one side of the dipole will always be emphasized at the expense of the other one. It is recommended that a common average reference is used to display the N170 component rather than the mastoids (which decrease the component substantially) or the nose (because of artifacts).

Paper rejected after reviews in *Human Brain Mapping*, no option to respond to comments. Then submitted to *Clinical Neurophysiology*.

Joyce, C.A., Schyns, P.G., Gosselin, F., Cottrell, G.W., Rossion, B. (2006). Early selection of diagnostic facial information in the human visual cortex. *Vision Research*, 46, 800-813.

In this study, we wanted to show that the N170 amplitude could be modulated by the task at hand, providing that the diagnostic information for this task is presented to the observer. We used the response classification images (and their inverse, non-diagnostic features) of "Bubbles" for gender and expression tasks, and asked observers to perform either of the two tasks. The N170 was larger for the difference between diagnostic and no-diagnostic features. This effect was indeed modulated (slightly) by the task at hand: if you have to categorize a face for expression, this difference is larger for diagnostic – non-diagnostic cues for expression than for gender, and vice-versa. Despite a strong manipulation and

clear behavioral effects, the N170 effects were not very large though, showing that the N170 amplitude is largely, although not completely, unaffected by the task at hand.

#### Paper first submitted to Vision Research

Jacques, C. & Rossion, B. (2006). The time course of visual competition to the presentation of centrally fixated faces. *Journal of Vision*, 6, 154-162.

This is a follow-up study to Jacques & Rossion (2004, Neuroreport). Here we show that the decrease of the N170 amplitude while processing a face can be observed even for stimuli that are presented at the fovea.

#### Paper first submitted to JOV

Jacques, C. & Rossion, B. (2006). The speed of individual face categorization. *Psychological Science*, 17, 485-492.

In this study, we introduced an original stimulation paradigm: we presented a continuous train of two faces alternating with each other at about 1.66 Hz. The rate was not fixed (duration of each face stimulus varied between 500 and 700 ms). Replacing a face by another face this way, without inserting a baseline, allowed us to almost cancel out the event-related responses that were not related to the difference between the 2 faces. This way, we erased the P1. We found a first negative deflection peaking at the exact same latency and topography as the N170, showing that individualization of faces takes place already at that latency. Using morphing, we also found that the response was larger when the 2 faces crossed a perceptual category boundary than when they remained within the same boundary (physical distance between the faces of the 2 pairs being equal).

#### Paper first submitted to Psychological Science

Jacques, C. d'Arripe, O., Rossion, B. (2007). The time course of the face inversion effect during individual face discrimination. *Journal of Vision*, 7(8):3, 1-9, http://journalofvision.org/7/8/3/, doi:10.1167/7.8.3.

If you present a face and then the same face again, we show that the N170 is reduced in amplitude (compared to a condition in which a new face is presented). Previous studies had found such effects but they were usually weak or not the focus of the study. Moreover, many studies fail to report face identity repetition effects on the N170. The interest of the present study is that we get a clear and large effect by increasing the duration of the first stimulus (several seconds), as in behavioral adaptation studies, and by using a very small ISI duration. We also change the size between the first and second stimulus of a pair, to remove pixelwise adaptation effects. Most importantly, we show for the first time that this effect is not present if the exact same faces are presented upside-down. We conclude that during the time-window of the N170, there is enough information accumulated by the system to be able to individualize faces.

#### Paper first submitted to JOV

14 Rossion, B., Collins, D., Goffaux, V., Curran, T. (2007). Long-term expertise with

artificial objects increases visual competition with early face categorization processes. *Journal of Cognitive Neuroscience*, 19, 543 – 555.

An extension of the study by Rossion et al. (2004) on visual expertise in the context of a visual competition paradigm. This study also shows one of the clearest effect of visual expertise with nonface objects on the perceptual encoding of faces, this time with large sample of participants (20 car experts, 20 novices). If you are busy fixating the picture of a car, the appearance of a face on the right or left of the car (which remains there) leads to a N170. This N170 is largely reduced in amplitude if you are a car expert as compared to a novice, particularly in the right hemisphere, suggesting that the perceptual encoding of the face suffers from the visual competition created by the fixation of the car picture. No difference is found between novices and experts if they fixate a cross or a non-recognizable pixellated car. We also show that this effect almost disappears if the car picture is removed before the appearance of the face, indicating that concurrent visual stimulation is critical to get a large effect. Irrespective of your interpretation of these findings (and attention is not a valid candidate, see Jacques & Rossion, 2007, Cerebral Cortex), while studies on visual expertise have been criticized for the small and non-replicable effects that they often report, this one truly reports big effects, in a simple paradigm.

Paper rejected in a couple of "high impact factor" journals, without review. Then submitted to *JOCN*.

Jacques, C. & Rossion, B. (2007). Electrophysiological evidence for temporal dissociation between spatial attention and sensory competition during human face processing. *Cerebral Cortex*, 17, 1055-1065.

In two studies (Rossion et al., 2004; 2007) summarized below, we found that when an expert with fixates a nonface object of expertise (Greebles or cars, respectively), the N170 in response to a face is significantly reduced in amplitude. Unsurprisingly, opponents of the expertise hypothesis claimed that this was merely an effect of attention: experts would pay more attention to their object of expertise than novices, therefore leading to a reduced N170 to faces. We had (many) reasons to believe that it was not correct, but we decided to tackle this issue directly. Here, we found that if you increase attention to the center, the N170 to a lateralized face is indeed reduced in amplitude, but this effects is additive to the reduction observed when it is a face that is fixated instead of a scrambled face. Most importantly, attention reduces not only the N170 but also the P1, while the competition effect (face vs. face compared to face vs. scrambled) concerns the N170 only. These findings suggest that the effect of visual expertise on the N170 in response to faces are not due to attention.

#### Paper first submitted to Cerebral Cortex

Jacques, C. & Rossion, B. (2007). Early electrophysiological responses to multiple face orientations correlate with individual discrimination performance in humans. *NeuroImage*, 36, 863-876. doi:10.1016/j.neuroimage.2007.04.016.

We aimed at understanding whether the N170 variations with inversion were meaningful with respect to the face inversion effect. We presented face stimuli at 12 orientations, from  $0^{\circ}$  to  $330^{\circ}$ , during a face identity matching task. ERP

analysis was made on the first stimulus, and behavioral measures on the second (target) stimulus. The results show that the variations of amplitude with stimulus rotation at he level of the P1 do not present the same pattern as the behavioral measures. However, after the P1, in the rising slope of the N170, one starts to see the same pattern emerging, with a "M"-shaped function across orientations both for behavior and EEG amplitude. The study suggests that the face inversion effect takes place at perceptual encoding, but not before the N170 time-window.

#### Paper first submitted to NeuroImage

Bentin, S., Taylor, M.J. Rousselet, G.A., Itier, R.J., Caldara, R., Schyns, P.G., Jacques, C. & Rossion, B. (2007). Much ado about nothing: controlling interstimulus perceptual variance does not abolish N170 face sensitivity, *Nature Neuroscience*, 10, 801-802.

A very frustrating experience. Following the publication of an incorrect paper in Nature Neuroscience, several groups of researchers who have been working on the N170 for years complained to the journal and wrote replies. The editors acknowledged to publish a response, but requested that all authors write a single 600 words common reply. This requested quite a lot of work and coordination, and prevented the authors to develop the full arguments to explain why Thierry et al.'s paper had to be entirely dismissed. Also, Thierry et al. were granted a reply, in which the limitations of their original study was hidden, and there were claims that there were no rules in the field according to which some electrodes should be used to measure the N170 appropriately. This made me determined to write something more extensive, hence the "10 lessons" review paper below, in order to explain why that paper was incorrect, and what lessons could be drawn for the field from such an unfortunate publication. Shlomo organized a meeting to discuss the issue in Jerusalem in 2008.

The problem here goes beyond this specific paper, because it shows that so-called high impact factor journals are sometimes more interested in publishing something incorrect if it makes a lot of noise (and it did!) than solid scientific work (often dismissed as "incremental"). As far as I know, none of the main contributors in N170 research was asked to review that paper, showing some serious flaws in the selection process. A lot of room for improvement there ...

REVIEW: Rossion, B. & Jacques, C. (2008). Does physical interstimulus variance account for early electrophysiological face sensitive responses in the human brain? Ten lessons on the N170. NeuroImage, 39, 1959-1979.

This long paper was written in reaction to unfortunate publication in Nature Neuroscience, in which the authors claimed that the larger N170 to faces than other visual stimuli was due to a methodological uncontrolled artifact in previous studies. Our long "10 lessons on the N170" paper was written after several groups of N170 researchers were denied by the journal the right to publish independent responses, and that the authors of the original paper did not acknowledge their mistake in their reply. Some of my colleagues tend to say that

Thierry et al.'s paper in Nature Neuroscience, even if it was incorrect, was only "controversial", or "useful", as a methodological warning for instance. From my part, I believe that this paper was not controversial, or useful in any way. It was incorrect, at many levels: the fact that authors who had no knowledge about this area of research and the N170 in particular could publish such a poor quality paper (in a so-called "high profile" journal), the lack of critical review process by experts in this area of research, the deliberate ignorance of the existing literature that contradicted the authors' claim, the measure of the N170 at wrong electrode sites so that it was not larger for faces than objects, the lack of explanation for a P1 effect, and the disrespectful attitude of the authors in their paper and their reply about other people's work in a field that they did not know.

Face perception an area of research that is confusing enough and has a lot of debates. It does not need such papers, which do not raise interesting "debates" but rather attempt to dismiss the phenomena that need to be explained. Anyway, I admit that our own review paper was written with a feeling of frustration, and it is certainly not a paper to read first if you are a beginner in this field  $\odot$ ! But at least this paper allowed to fix the problems created by Thierry et al (i.e. rejection of grant applications and papers on the basis that the N170 would be an uncontrolled artefact). Our review paper also provided us with the opportunity to make a number of points regarding the functional interpretation of the N170, and I hope that in the end it makes a useful contribution to the research community in this area.

#### Paper first submitted to NeuroImage

Since we published this NeuroImage paper, I have not pursued an interest in what is not a real debate for me, and rather concentrated on more important issues regarding this N170 component. I have in fact declined invitations to debate about this at conferences with the first author of the Nature Neuroscience paper and declined to review any submission related to this. But other authors have done some interesting work on this, and for the readers interested in this issue, see for instance:

Eimer, M. (2011). The face-sensitivity of the N170 component. Frontiers in Human Neuroscience, 5:119.

Schendan HE, Ganis G. (2013). Face -specificity is robust across diverse stimuli and individual people, even when interstimulus variance is zero. Psychophysiology. 50, 287-291.

Ganis G, Smith D, Schendan HE. (2012). The N170, not the P1, indexes the earliest time for categorical perception of faces, regardless of interstimulus variance. Neuroimage. 62, 1563-1574.

Maurer, U., Rossion, B., McCandliss, B. (2008). Category specificity in early perception: face and word N170 responses differ in both lateralization and habituation properties. Frontiers in Human Neuroscience, 2:18.

This study contrasted N170 responses to words and faces within the same subjects, examining both category-level habituation and lateralization effects.

ERP responses to a series of different faces and words were collected under two contexts: blocks that alternated faces and words vs. pure blocks of a single category designed to induce category-level habituation. Global and occipito-temporal measures of N170 amplitude demonstrated an interaction between category (words, faces) and block context (alternating categories, same category). N170 amplitude demonstrated class-level habituation for faces but not words. Furthermore, the pure block context diminished the right-lateralization of the face N170, pointing to class-level habituation as a factor that might drive inconsistencies in findings of right-lateralization across different paradigms. No analogous effect for the word N170 was found, suggesting category specificity for this form of habituation. Taken together, topographic and habituation effects suggest distinct forms of perceptual processing drive the face N170 and the visual word form N170.

# Paper first submitted to Frontiers in Human Neuroscience (not 100% sure!)

Caharel, S., d'Arripe, O., Ramon, M., Jacques, C., Rossion, B. (2009). Early adaptation to unfamiliar faces across viewpoint changes in the right hemisphere: evidence from the N170 ERP component. Neuropsychologia, 47, 639-643.

This is the first study showing a reduction of the N170 for a repeated face identity when there is a change of viewpoint between the 2 faces.

A respected colleague of mine likes to cite it as the only paper showing an effect of face identity on the N170, but I disagree: there are many others, from our lab, or other labs, and when viewpoint does not change, we always change at least the size of the stimuli that are repeated. Anyway, here we asked whether the larger N170 to unrepeated compared to immediately repeated faces would still hold despite a change of viewpoint between the two faces. One previous study suggested that it was not the case, but we were not convinced by an absence of effect and used a sensitive paradigm with long duration of presentation for the adapter and a short delay before the presentation of the target face. Even across a 30° change of viewpoint, there was still an identity adaptation effect, but only on the right N170.

#### Paper first submitted to Neuropsychologia

Jacques, C., Rossion, B. (2009). The initial representation of individual faces in the right occipito-temporal cortex is holistic: electrophysiological evidence from the composite face illusion. Journal of Vision, 9(6):8, 1–16, http://journalofvision.org/9/6/8/, doi:10.1167/9.6.8.

Here the identity adaptation paradigm was used to test the hypothesis that as early as the individual face was perceptually encoded (N170 peak, see Jacques et al., 2007, JOV), this encoding is holistic. Observers fixated the top halves of two sequential faces to match. We found that even when the bottom halves only changed identity, eliciting the visual illusion of a change on the fixated top half,

the N170 was larger in amplitude than when there was no change of identity. This effect disappeared if the two halves were spatially misaligned. This study therefore demonstrates that the first individual face representation that is perceived is holistic rather than based on independently perceived local parts.

#### Paper first submitted to JOV

Caharel, S., Jiang, F., Blanz, V., Rossion, B. (2009b). Recognizing an individual face: 3D shape contributes earlier than 2D surface reflectance information. NeuroImage, 47, 1809-1818.

A very clear and interesting finding to me, illustrating nicely the interest of the ERP approach. We used our identity adaptation paradigm, but manipulated the kind of information that conveyed the identity of the face: either 3D shape, or 2D surface reflectance (color/texture), or both simultaneously. Behaviorally, participants discriminated faces better and faster when the two kinds of information were present, as in previous studies. However, ERP data told a different story: at the level of the N170, a significantly larger amplitude than the repeated face identity condition was found only when 3D shape differed between the adapter and target face. When surface reflectance alone was different, there was no significant effect. However, at a later component (P2), shape and reflectance elicited an effect of the same magnitude, while combining the two kinds of diagnostic information elicited the largest effect (in line with behavior). Hence, the early encoding of an individual face percept seems to be based primarily on 3D shape, not surface reflectance.

#### Paper rejected without reviews in Cerebral Cortex. Then submitted to NeuroImage.

Jacques, C., Rossion, B. (2010). Misaligning face halves increases and delays the N170 specifically for upright faces: implications for the nature of early face representations. Brain Research, 1318, 96-109.

Don't get confused ... This study is not really about the composite face effect, which is an effect that reflects the perception of individual faces and that was tested in another study (Jacques & Rossion, 2009). Here we extended the study of Letourneau & Mitchell (2008), by testing the effect of misaligning horizontally the two halves of face (top and bottom). We replicated their observation that this misalignment (paradoxically) increases the latency and the amplitude of the N170, particularly in the right hemisphere, just like inversion. But we used several control conditions to show that this observation cannot be accounted for by a general effect of spatial misalignment of visual patterns. Interestingly, we also found that it does not hold for inverted faces. These observations support the view that the early face representation activated in the human brain at the level of the N170, is that of a global upright face pattern.

#### Paper first submitted to Brain Research

Kuefner, D., Jacques, C., Prieto, E.A., Rossion, B. (2010). Electrophysiological correlates of the composite face illusion: disentangling perceptual and decisional components of holistic face processing in the human brain. Brain and Cognition, 74, 225-238.

Here we used the composite face effect, a well-known measure of holistic face perception, in combination with an oddball paradigm in ERPs and a Go/Nogo response, asking participants to detect rare changes of identity to the top halves (but ignore changes to the bottom halves). Our idea was to show that even when human observers do NOT respond behaviorally to changes of identity on the bottom halves of faces, and do not elicit a lateralized readiness potential (LRP), there is an electrophysiological marker of holistic face perception in the sense of a larger N170 to these trials (relative to the repetition of the exact same face, see Jacques & Rossion, 2009). It seems quite obvious to me (and many researchers) that the composite effect reflects a perceptual effect, but strangely enough some authors have argued that its locus is decisional, based on behavioral data. The present study provides direct evidence against this claim.

Paper rejected after reviews in Neuropsychologia. One of the first time in my career that we were allowed to respond and yet the paper was rejected. Did not agree with the decision there, but this happens... Then submitted to Brain and Cognition.

Kuefner, D., de Heering, A., Jacques, C., Palmero-Soler, E., Rossion, B. (2010). Early visually evoked electrophysiological responses over the human brain (P1, N170) show stable patterns of face-sensitivity from 4 years to adulthood. Frontiers in Human Neuroscience. 3:67. doi:10.3389/neuro.09.067.2009.

A study in which we show that the P1 and N170 do not change specifically for faces between 4 years of age and adulthood, contrary to what was stated in previous studies. There are indeed major changes in the basic response properties of these components (reduction of latency and amplitude, lateralization of posterior topography), but they are found for any kind of visual stimulus for the P1, and for both faces and objects (cars) for the N170. A larger N170 for faces than cars, with a right lateralization, is found in younger children and does not appear to increase with age.

Paper first submitted to *Frontiers in Human Neuroscience* (special issue on Developmental Cognitive Neuroscience)

Caharel, S., Jacques, C., d'Arripe, O., Ramon, M., & Rossion, B. (2011). Early electrophysiological correlates of adaptation to personally familiar and unfamiliar faces across viewpoint changes. Brain Research, 1387, 86-98.

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We previously found that a N170 face identity adaptation effect over right electrode sites even when the adapter and target faces are presented under

different viewpoints (Caharel et al., 2009). Here we hypothesized that it would increase when presenting pictures of personally familiar faces. This would have provided evidence that the behavioral advantage provided by familiarity in individual face matching was related to perceptual encoding. Instead, we found that the effect disappeared for familiar faces: the N170 was no longer different in amplitude for repeated and unrepeated face identities! Interestingly though, an effect appeared on the left hemisphere N170 for familiar faces. At much later latencies, closer to the behavioral response, we found a larger effect for familiar than unfamiliar face.

#### Paper first submitted to Brain Research

Alonso-Prieto, E., Caharel, S., Henson, R.N., Rossion, B. (2011). Early (N170/M170) face-sensitivity despite right lateral occipital brain damage in acquired prosopagnosia. Frontiers in Human Neuroscience. Front. Hum. Neurosci. 5:138. doi: 10.3389/fnhum.2011.00138

We report a face-sensitive N170 effect over the right hemisphere of the prosopagnosic patient PS, despite extensive damage in this hemisphere and no evidence of right OFA activation in numerous previous studies. The N170 also shows the typical amplitude increase and delay to inverted faces. A M170 is also disclosed in a MEG study. Interestingly, the component is absent in the left hemisphere, where the patient has another lesion in the middle fusiform gyrus (no left FFA). This observation suggests that the OFA is not strictly necessary to observe early sensitivity to faces in the right occipito-temporal cortex.

#### Paper first submitted to Front. Hum. Neurosci.

Rossion, B. & Caharel, S. (2011). ERP evidence for the speed of face categorization in the human brain: disentangling the contribution of low-level visual cues from face perception. Vision Research, 51, 1397-1311.

This is a study that we - or others - should have done a long time ago ... It is very simple, but the result is important to understand the nature of the N170. We presented faces, cars, and their respective phase-scrambled versions (phase-scrambled faces and phase-scrambled cars). Pictures of faces and cars were equalized for luminance but were left deliberately uncontrolled for other potential differences in power spectrum and color. We replicated both the larger P1 and N170 to faces than cars. However, the P1 face effect was equally large for phase-scrambled stimuli: it was larger for phase-scrambled faces than phase-scrambled cars! This, even though these stimuli could not be perceived as meaningful categories at all. In contrast, the N170 face effect was found only for non-scrambled versions of the stimuli. Thus, this study shows that even if a preferential response to faces can be found before the N170 onset, namely during the P1 time-window, it should not be interpreted as reflecting the perception of a face.

I like to use the findings of this study to say that it shows the border between

*low-level and high-level vision (i.e. interpretation)* 

#### Paper first submitted to Vision Research

Jonas, J., Descoins, M., Koessler, L., Colnat-Coulbois, S., Sauvee, M., Guye, M., Vignal, J-P., Vespignani, H., Rossion, B., Maillard, L. (2012). Focal electrical intracerebral stimulation of a face-sensitive area causes transient prosopagnosia. *Neuroscience*, 222, 281-288.

The paper is not mainly about the N170 component: it reports a case of transient failure to recognize faces, during electrical stimulation of a face-selective area of the right inferior occipital cortex (see the videos on our website). However, inside this region, we recorded an intracerebral N170, reversing polarity (P170). It suggests that one of the sources, perhaps a dominant source, of the scalp N170 is located in the lateral part of the right occipital cortex. The polarity reversal – indicator of a local generator - could be observed thanks to the approach used (depth electrodes, or stereotactic EEG rather than subdural grids of electrodes).

Paper rejected in a couple of "high impact factor" journals, without review. Then rejected after review at *Journal of Neuroscience*, no opportunity to respond. One reviewer wrote that this observation was "trivial", only to see the journal publish a similar paper a few months later  $\otimes$ 

Our paper was then submitted to *Neuroscience* and accepted after constructive comments

Kovács, G., Zimmer, M., Volberg, G., Lavric, I., Rossion, B. (2013). Electrophysiological correlates of visual adaptation and sensory competition. *Neuropsychologia*, 51, 1488-1496.

This paper follows an idea and work generated essentially by Gyula Kovács and his colleagues, based on complementary work that Gyula and I did on adaptation on competition effects on the N170, respectively. The N170 was obtained for two faces or for a face and a phase-scrambled face in three different conditions: (1) a first stimulus (S1) closely followed by a second one (S2); (2) S1 remaining on screen when S2 appeared (3) or S1 and S2 having simultaneous onset and offset times. There was a stimulus specific reduction of the N170 when the onset of S1 preceded the onset of S2. In contrast, simultaneous presentation of the two stimuli had no specific effect on N170. This suggests either that competition does not lead to early repetition suppression or that the absence of a larger N170 response to two simultaneously presented face stimuli compared to a single stimulus reflects competition between overlapping representations. Overall, these results show that the asynchronous presentation of S1 and S2 is critical to observe stimulus specific reduction of the N170, presumably reflecting adaptation-related processes.

#### Paper first submitted to Neuropsychologia

Caharel, S., Ramon, M., Rossion, B. (2014). Face familiarity decisions take 200ms in the human brain: electrophysiological evidence. *Journal of Cognitive Neuroscience*, 26, 81-95.

This is not a paper focusing on the N170, but on a different approach, inspired by Simon Thorpe and colleagues' ERP work using the Go/Nogo paradigm. We tested participants with pictures of personally familiar faces (classmates) in a study asking them to raise their finger for familiar (Go) faces only (unfamiliar = No-go). Go (familiar) and (Nogo) responses elicited clear differential waveforms from 210 milliseconds (ms) onward, this difference being first observed at right occipito-temporal electrode sites. There was also a small N170 difference for familiar and unfamiliar faces but it vanished with stimulus repetition. This observation indicates that accumulation of evidence within the first 200 ms post stimulus onset is sufficient for the human brain to decide whether a person is familiar based on his/her face, a time frame that is compatible with sensitivity to individual faces on the N170 and puts strong constraints on the time-course of face processing.

#### Paper first submitted to JOCN

Rossion, B. (2014). Understanding face perception by means of human electrophysiology. *Trends in Cognitive Sciences*, 18, 310-318.

This is a review paper that goes beyond the N170, but the main part of the paper is about this N170 component. I argue that, as far as ERPs are concerned, the focus in face perception research should be on this N170 component because face perception is a process generally accomplished by 200 ms following stimulus onset. Also, the N170 precedes potential saccadic eye movements. I suggest that the 100-200 ms time-window witnesses the transition between low-level and high-level vision, the N170 component correlating with the conscious interpretation of a visual stimulus as a face. This initial face representation is rapidly refined as information accumulates during the N170 time-window, allowing to individualize faces. In complementary boxes, I

- (1) Discuss the issue of controlling for low-level visual differences between faces and nonface stimuli, or various face stimuli, suggesting that a control by generalization is better than a control by elimination (of diagnostic cues);
- (2) Qualify the power and interest of single-trial analyses in EEG research, which could be interesting ins psecific cases but should not replace standard ERP research measuring averaged components' amplitudes and latencies;
- (3) Discuss the neural sources of the N170 component, and the need to gather information about these sources from intracerebral recordings of the human brain.

#### Paper first submitted to TICS (invitation)

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Caharel, S., Collet, K., & Rossion, B. (2015). The early visual encoding of a face (N170) is viewpoint-dependent: a parametric ERP-adaptation study. *Biological Psychology*, 106, 18-27

This is an extension of the studies performed by Stéphanie Caharel on this face adaptation paradigm with changes of head views (Caharel et al., 2009; 2011), but this time, we used a parametric manipulation with 6 head rotations from a full-front face adaptor. The results show that the N170 adapts to viewpoint (independently of identity) for a 0° change and less so to a 15° change. Then there is no adaptation. And adaptation to identity (i.e. difference between same and different faces repeated) resists until 30° viewpoint change.

The first observation shows that a face is encoded in a view-dependent manner, being matched to either a full-front or a profile face view: a 15° view lies in between. The second one shows that individual face representations activated as early as the peak of the N170 generalize partially across views (up to 30°).

Paper first submitted to Biological Psychology

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