CHAPTER 5

The N170: Understanding the Time Course of Face Perception in the Human Brain

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Abstract

This chapter reviews the contribution of electromagnetic measures, mostly event-related potentials (ERPs), to our understanding of the time course of face processing in the normal adult brain, with a focus on the 100–200 ms time window after stimulus onset, that is, during during the occipitotemporal component termed the N170. It first describes the N170 component, how it can be defined, and its relationship to the vertex positive potential (VPP) response to faces that was reported prior to the N170 in the literature. It then addresses the question of the origin of the largest N170 to faces in terms of electroencephalographic (EEG) signal, neural sources, and functional processes that lead to this effect. It also discusses the controversial issue of whether the N170 reflects underlying processes that can be at least partly recruited for processing nonface objects following extensive visual experience with these objects. The chapter summarizes the evidence showing that the N170 reflects both the initial basic-level categorization of the stimulus as a face through the activation of neural face representations and the coding of individual face representations. It then briefly discusses why the N170 may be a critical time window for other types of face categorizations before summarizing the chapter and addressing the question of how the N170 can be taken as a tool to clarify the dynamics and the nature of early face processes in future research.

Keywords: event-related potential, N170, face perception, perceptual processing, occipito-temporal component

This chapter reviews the functional properties of a human visual event-related potential (ERP) component, the N170, which has been associated with the perceptual processing of faces. A face can be detected in a visual scene extremely rapidly (e.g., Fei-Fei et al., 2007; Lewis & Edmonds, 2003; Rousselet et al., 2003), and a familiar person can be identified from his or her face in a few hundred milliseconds (e.g., Young et al., 1985). Various kinds of information can also be extracted quickly and efficiently from the face in order to categorize the person's gender, facial expression, ethnic origin, direction of gaze, and so on. (Bruce & Young, 1998). Since the early 1970s, with the huge increase in the amount of empirical work on face processing (Ellis, 1986), experimental psychologists and psychophysicists have aimed at clarifying the nature of the facial cues that are diagnostic to process faces (e.g., Haig, 1985), how these cues are integrated into global face representations (e.g., Sergent et al., 1984; Young et al., 1987), and how face processes and representations can be distinguished and organized in an information processing framework (e.g., Bruce & Young, 1986).

However, while behavioral studies have access only to the input and output of the system, the diagnostic information for face categorization is dynamically processed in the human brain in the period between the onset of the visual stimulation and a behavioral response several hundreds of milliseconds later. Clarifying the exact time course of face processes is a major goal of cognitive neuroscience. Because of their high temporal resolution, noninvasive electromagnetic measures, mostly ERPs but also event-related magnetic fields (ERMFs—in magnetoencephalography [MEG]) recorded on the human scalp, can greatly contribute to reach this objective. Event-related potentials to simple visual stimulation with a few electrodes were extensively investigated and described in the 1960s and 1970s (see Regan, 1989), but it is only since the late 1980s that ERPs to complex visual stimuli, in particular faces, have been systematically studied (Bötzel & Grüsser, 1989; Jeffreys, 1989).

The goal of this chapter is to assess the contribution of electromagnetic measures, mostly ERPs, to our understanding of the time course of face processing in the normal adult brain, with a focus on the 100–200 ms time window after stimulus onset, that is, during the occipitotemporal component termed the N170. Currently, more than hundreds of studies refer to the N170 component, without any published review. Reviewing all the findings and issues raised by these studies is clearly beyond the scope of this chapter. Therefore, for sake of clarity and in accordance with the objective of this volume, we have chosen to concentrate on summarizing and discussing *basic* issues regarding the N170 in the normal adult human brain. We will first describe the N170 component, how it can be defined and its relationship to the vertex positive potential (VPP) response to faces that was reported prior to the N170 in the literature (see “The Early ERP Studies of Face Processing and the N170 Face Effect”). Then we will address the question of the origin of the largest N170 to faces in terms of EEG signal, neural sources, and functional processes that lead to this effect (see the section “Why Is the N170 Larger to Faces?”). We will also discuss the controversial issue of whether the N170 reflects underlying processes that can be at least partly recruited for processing nonface objects following extensive visual experience with these objects (see the section “Are Early Face Processes Flexible?”). In the fourth section (“The N170: A Tool to Disentangle and Clarify the Time Course of Face Processes”), we will summarize the evidence showing that the N170 reflects both the initial basic-level categorization of the stimulus as a face through the activation of neural face representations *and* the coding of *individual* face representations. We will then briefly discuss why the N170 may be a critical time window for other types of face categorizations before summarizing this chapter (see the section “Summary, Questions to Clarify, and Future Directions”) and addressing the question of how the N170 can be taken as a tool to clarify the dynamics and the nature of early face processes in future research.

The Early ERP Studies of Face Processing and the N170 Face Effect

The VPP as the Vertex Positive Counterpart of the N170

The first systematic ERP studies of face processing (e.g., Bötzel & Grüsser, 1989; Jeffreys, 1989; Jeffreys et al., 1992; Seek & Grüsser, 1992) reported a large positive potential peaking at the vertex between 140 and 180 ms following the presentation of a face stimulus (Figure 5.1a), termed the *vertex positive potential* (VPP) (following Jeffreys et al., 1989). In reviewing the response properties of the VPP, Jeffreys (1996) emphasized its larger amplitude in response to faces than other visual object categories and noted that the VPP presented a negative counterpart at bilateral occipitotemporal sites, suggesting sites of origin in areas of the temporal cortex (Figure 5.1a). However, the investigation of the VPP was emphasized in these initial studies because few if any electrodes were located on posterior lateral temporal regions of the scalp. Moreover, most of these studies used a mastoid reference located closely to the electrode sites picking up the occipitotemporal side of the dipolar activity. As a result, the amplitude of the occipitotemporal negativity was attenuated and the VPP increased, as can be demonstrated even with a large array of electrodes (see Joyce & Rossion, 2005; Figure 5.1b).

In subsequent studies of face stimulation, the use of a different reference (e.g., common average, nose; Bentin et al., 1996; Bötzel et al., 1995; George et al., 1996) to analyze the ERPs, and the availability or EEG recording systems with a larger number of electrodes covering the whole scalp favored the investigation of the occipitotemporal negative counterpart of the VPP, peaking at about 160–170 ms with a larger amplitude in the right hemisphere (Bötzel et al., 1995; George et al., 1996). This negativity was termed the N170 by Bentin and colleagues (1996).

Over the past 15 years, hundreds of ERP studies of face processing referring to the N170 component have been published. Magnetoencephalographic scalp recordings revealed a “M170” component with response properties similar to those of the N170 (e.g., Liu et al., 2000; Halgren et al., 2000; Sams et al., 1997). The advantage of focusing on the N170 rather than on the VPP is twofold. First, the electrodes recording the N170 on the scalp are closer to the neural generators of the component. Second, studying the N170 rather than the VPP allows

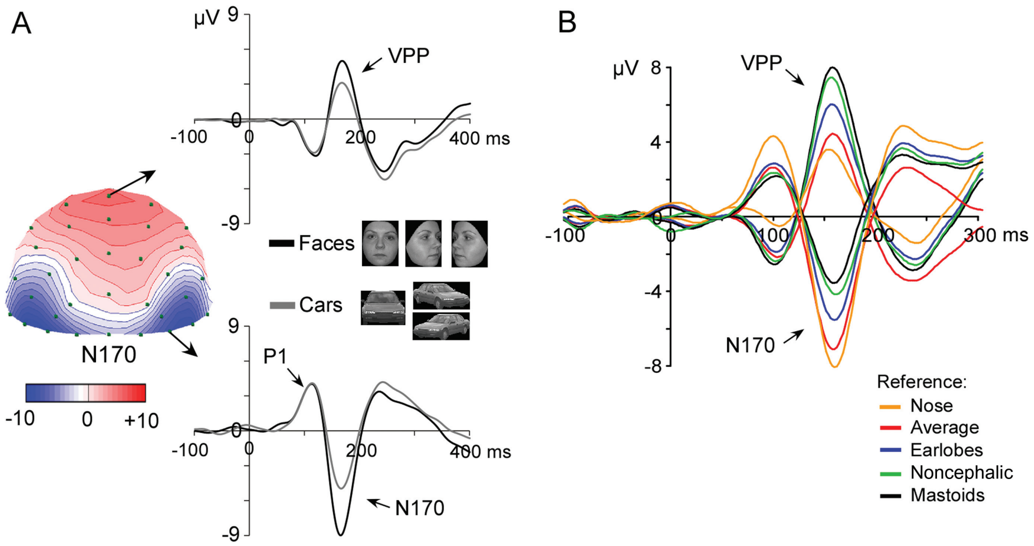

Fig. 5.1. (A) A typical N170 recorded from posterior lateral electrode sites following the presentation of faces and nonface objects (pictures of cars). It peaks at about 160–170 ms following stimulus onset and is most prominent at the lowest occipitotemporal electrode sites, usually maximal on channels P8(T6) or PO8, or on lower channels in this area if available. It is associated with a temporally coincident positivity on the vertex (Cz), the vertex positive potential (VPP). The VPP shows the same response properties as the N170 and largely reflects the projection of the occipitotemporal dipolar sources to the vertex. The data presented are grand averages of 20 subjects presented with full-front and three-quarter profile pictures averaged together (180 trials/condition/subject, common average reference; from Rossion & Jacques, 2008). (B) The inversion of polarity between the N170 and VPP. The relative amplitude of the two "faces" of the component shows an inversely proportional relationship depending on the location of the reference electrode (see Joyce & Rossion, 2005).

investigation of the hemispheric lateralization of face processes (Joyce & Rossion, 2005).

The N1, the N170, and the N170 Face Effect

In the jargon of ERP researchers, the N170 corresponds to the visual N1 component: It is the first negative deflection on posterior scalp regions, following early posterior visual components C1[1] (peak ~70 ms) and P1 (peak ~100 ms), which can be observed in response to any visual stimulus. This N1 has a peak latency of 130–200 ms (see, e.g., Clark et al., 1995; Vogel & Luck, 2000; Chapter 4, this volume). However, the N1 is particularly large in response to pictures of faces and peaks on average at about 160–170 ms for these stimuli. Furthermore, the N170 marks the earliest, strongest, and most reliable difference in amplitude on the scalp between faces and nonface objects (e.g., Bentin et al., 1996; Bötzel et al., 1995; Rossion et al., 2000).

Together with its peak latency and its occipitotemporal topography, this larger amplitude to faces than to any other object category is what *defines* the N170 in the literature (Figure 5.1a). While some ERP researchers have referred to an N1 component in response to objects versus an N170 in response to faces (Carmel & Bentin, 2002; Itier & Taylor, 2004a), we believe that it is most appropriate to use the same label for the ERP component elicited by faces and objects. In short, the posterior lateral N1 component recorded to any visual stimulation varies in amplitude for different stimuli (see Rossion et al., 2000) and is particularly enhanced in response to faces. An important question is, of course, whether this face effect is due to stronger activation of the *same* neural sources that are recruited for nonface visual stimuli or to the addition of *other* sources specific to faces. As we will see in the next section, ERP researchers can address this issue only indirectly. Moreover, for sake of clarity in this field, the answer to this question should not change the terminology given to the basic ERP component that is used as a marker of high-level visual processes: It should either be the N1 or the N170 for all visual stimuli. Because of peak latency variability, the term *N1* may seem more appropriate. However, the term *N170* has become widely used in the face processing literature for the past 15 years. For this reason, we will refer to the *N170* (for both faces and nonface objects) and to the *N170 face effect* (the largest amplitude to faces) in the remainer of the chapter.

Why Is the N170 Larger to Faces?

While the N170 is systematically larger in amplitude for pictures of faces than for other object categories tested, there are also substantial N170 amplitude differences among nonface object categories (Itier & Taylor, 2004a; Rossion et al., 2000). In particular, pictures of highly familiar objects such as cars elicit a quite large N170 component, yet systematically smaller than the N170 to faces (Rossion & Jacques, 2008). From the published literature, it is currently impossible to quantify the magnitude of the N170 face effect because the amplitude of the N170 varies substantially among participants, and the categories of stimuli compared to faces, as well as the tasks that are used (passive viewing, one-back detection task, orientation judgment), differ greatly among studies. In fact, it is impossible to identify a "typical" ERP paradigm used to assess face and object differences at the level of the N170 in the literature, unlike what is done in functional magnetic imaging resonance (fMRI) studies to localize the areas of the visual cortex responding preferentially to faces (e.g., the so-called *fusiform face area* [FFA]; Kanwisher et al., 1997). Moreover, it is difficult to quantify the magnitude of the N170 face effect because there are other methodological parameters that can greatly influence this effect (e.g., the location of the reference electrode; see Joyce & Rossion, 2005; Figure 5.1) and that also vary substantially among studies. Yet, unless one reduces the N170 component amplitude through extremely severe low-pass filtering (Schweinberger et al., 2004) or measures its amplitude at the wrong electrode sites (e.g., medial occipital; see Rossion & Jacques, 2008), the N170 is systematically and substantially larger in response to faces than to nonface visual stimuli.

Why is the N170 larger for faces? Interpreting a differential amplitude of a scalp ERP component between two conditions is not straightforward, and in the case of the N170 face effect there are several issues to consider. The first issue refers to the origin of the effect in terms of EEG signal. This will be examined in the next section.

The N170: Time-Locked Increase in EEG Amplitude Rather Than Intertrial Phase Realignment

According to the traditional view of the generation of ERP components, the N170 originates from a massive synchronized increase in postsynaptic neural activity time-locked and phase-locked to stimulation onset, superimposed on background electrophysiological activity unrelated to the stimulation. In this framework, the N170 face effect simply reflects a *larger* increase in neural activity to faces compared to objects. This leads to a larger increase in EEG amplitude at a constant latency and polarity on the scalp for faces. Alternatively, the N170 face effect may be simply due to face stimuli eliciting an electrophysiological response at a more consistent latency from trial to trial compared to objects. This smaller intertrial latency jitter in response to faces would correspond either to a lower variance in the peak latency of the N170 from trial to trial or to a more precise phase resetting of ongoing EEG oscillations (i.e., preceding the stimulus; see Chapter 2, this volume). This phenomenon would also lead to a larger N170 after averaging in the time domain (Sayers & Beagley, 1974) without necessarily being associated with an increased recruitment of neural sources compared to nonface objects. This is an interesting idea because it has often been claimed that, compared to many object categories, faces form a particularly visually homogeneous category (Damasio et al., 1982), thus potentially leading to a better alignment of visual responses to members of the face class than to nonface objects. Moreover, it has been proposed that the visual N1 component to simple stimuli can indeed be largely generated by such a phase resetting of EEG ongoing oscillations in the alpha range (Makeig et al., 2002; but see Mazaheri & Jensen, 2005; Sauseng et al., 2007).

However, there is currently no evidence in favor of the phase-resetting model as accounting, even partly, for the N170 component and for the N170 face effect. That is, the largest N170 to faces is associated with a massive increase of power in the 5 to 15 Hz band time-locked to stimulus onset (Rousselet et al., 2007), which would not be observed in a case of pure phase resetting. Moreover, the supposedly larger visual homogeneity between exemplars of the face category than the nonface category (Damasio et al., 1982) is also irrelevant with respect to the N170 face effect: Most ERP studies have compared ERPs in response to faces and to members of the *same* nonface object class (e.g., cars), with exemplars of the nonface object class being highly similar (see Rossion & Jacques, 2008).

Even though the N170 face effect is largely due to a time-locked larger increase in EEG amplitude for faces, comparing faces to objects with various shapes, textures, and colors may possibly increase the N170 face effect artificially and create latency differences between categories in the averaged N170 response. For instance, when homogeneous pictures of faces are compared to pictures of nonface objects with various shapes, there appears to be an increase in the peak *latency* of the averaged N170 as well as a *widening* of the component for nonface objects (e.g., Itier & Taylor, 2004a), two phenomena that could be due to an increase in latency jitter between trials (Regan, 1989; Figure 5.2). This caveat can be circumvented by comparing the N170 to face and nonface stimuli of similar visual homogeneity, with the ERP response being averaged separately for each category, as in the majority of N170 studies (Rossion & Jacques, 2008). In these conditions, when visual stimuli are segmented from the background scene, the N170 is consistently larger in amplitude to faces than objects, but it does not peak earlier and the component is not wider for nonface objects (Figure 5.1).

Do We Need a "Face Localizer" Approach in N170 Studies?

A question of interest is whether it would be possible, or even worthwhile, to design a typical face localizer paradigm that should be used across all or most studies to identify the N170 face effect, similar to fMRI studies prelocalizing the "face areas." The answer to this question is probably negative for several reasons. First, a face localizer paradigm as it is currently used in most fMRI studies is inappropriate, as it compares a set of visually homogeneous faces to various kinds of object categories (see Rossion & Jacques, 2008). Moreover, in traditional fMRI face processing studies, it is our experience that a one-back matching task commonly used in

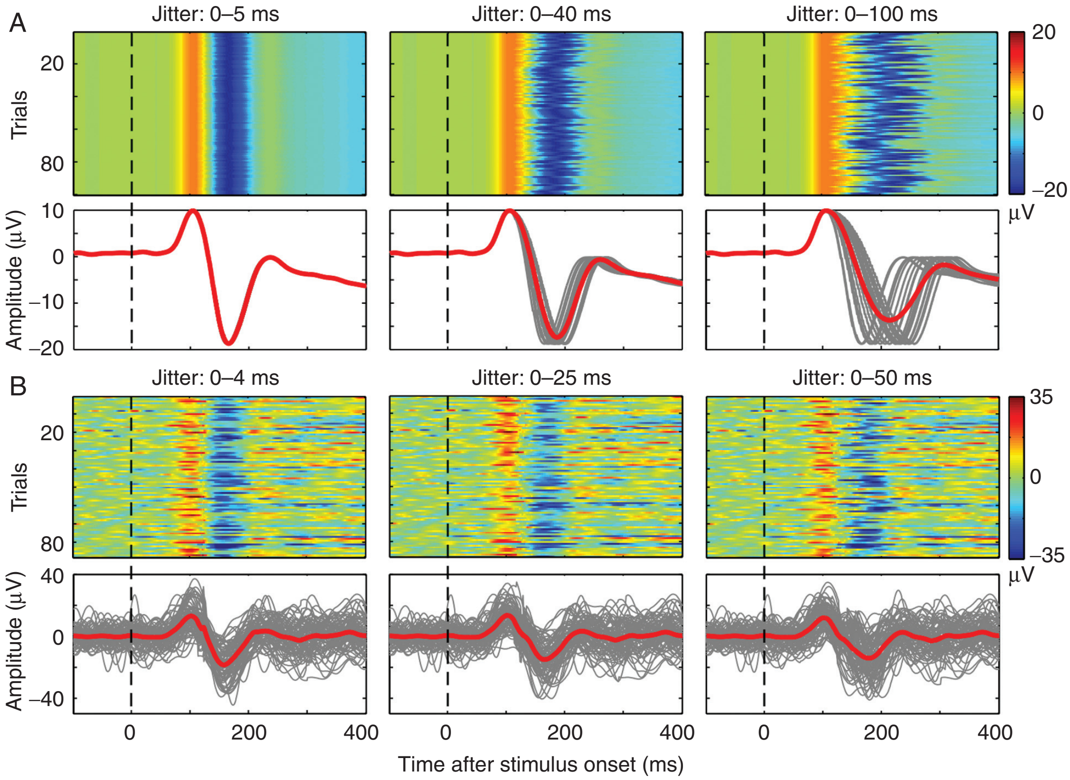

Fig. 5.2. Effect of increasing intertrial time jitter in the peak latency of the N170. (A) Simulation of jitter in the slope between the P1 peak and the N170 peak based on a grand averaged ERP response to face stimuli. The jitter was generated by randomly stretching the ERP from 100 to 160 ms after stimulus onset in the range of 0–5 ms (left), 0–40 ms (middle), and 0–100 ms (right). The upper row shows ERP images (trials x time, color-coded for amplitude; number of trials generated = 100) of the jitter simulation. The lower row shows a subset of individual trials (thin gray traces) as well as an average of 100 simulated trials (thick red trace). (B) Simulation of intertrial jitter using real EEG data. The simulated data were generated by adding sections of a grand averaged ERP response corresponding to the P1, N170, and P2 to 90 individual real EEG epochs containing no ERP. The ERP section corresponding to the N170 component was randomly jittered in latency (range, 0–4, 0–25, and 0–50 ms) and in amplitude before it was added to the EEG background. Note in both simulations the reduction of amplitude, the latency increase, and the smearing of the N170 as time jitter increases. Upper row: ERP images of the 90 simulated trials. Lower row: the 90 individual trials (thin gray traces) and the average of these trials (thick red trace).

so-called localizer paradigms (e.g., Kanwisher et al., 1997) is unbalanced: It is harder for faces than objects. Second, one would have to identify a specific category of stimuli that could be adequately compared to faces in terms of complexity, symmetry, familiarity, and so on. This issue has plagued the behavioral face processing literature for a long time, and experimenters generally admit that there is no such perfect control stimulus. Consequently, various stimuli are used in different studies (cars, houses, birds, chairs, etc.). Third, while regions such as the FFA can be disclosed in the individual human brain only by using a statistical criterion to estimate a differential level of activation to faces and objects, the N170 can be readily identified as a large voltage change (with respect to the reference electrode) in a single condition (i.e., face stimulation), without the need to make a statistical comparison with a nonface object stimulation. Moreover, considering the limited spatial resolution of scalp ERPs/ERMs, there is currently no evidence that the topographical distribution of the N170/M170 in response to faces is different than the topography of the N170/M170 face effect (Rossion et al., 2003). In addition, most ERP studies are interested in testing hypotheses about the time course of faces processes using the N170 as a tool, and simply need to identify the component in response to different face stimulations without asking direct questions about the face specificity of the effects. Finally, limiting analysis to spatiotemporal regions specific to faces may hide potentially interesting effects occurring outside of face-specific spatiotemporal windows as identified by the localizer. This is particularly problematic when experimental effects that are specific to faces occur outside such spatiotemporal windows.

For all these reasons, we believe that using a face localizer approach, which may be useful but not without its own problems in fMRI studies (see Friston et al., 2006; Saxe et al., 2006), is unnecessary for ERP studies of face processing. Yet, if such a typical paradigm to identify the N170 effect had to be used in order to address questions concerning only face-specific processes during the N170 time window, several issues are worth considering. First, the ERP response to pictures of faces should be compared to the ERP response obtained by averaging EEG segments elicited by pictures of the same visually homogeneous object category, such as cars, rather than mixing different object classes together. If time is not too constrained, several object classes can be used, provided that that the ERP averages are determined separately for each object class (e.g., Rossion et al., 2000). Second, in order to remove potential ERP effects due to low-level visual differences between faces and nonface objects, these stimuli should also be presented as phase-scrambled versions, controlling for the global luminance, contrast, and power spectra of the images (i.e., scrambled faces and cars; see Figure 5.3). The interaction between shape stimuli and their scrambled counterpart (faces–scrambled faces; cars–scrambled cars) should reveal the spatiotemporal time window that is most sensitive to faces. Third, all conditions should be randomized within each block of trials in order to avoid differential repetition effects and attentional confounds. Fourth, participants should perform an active task (e.g., one-back matching) to maintain their attention level quite high throughout the face localizer experiment, with a task that is equally difficult for all categories of stimuli. Finally, given the high temporal resolution of the method, identifying the N170 face effect on the scalp requires a spatio*temporal* definition: Which exact time window, for each electrode and in each individual participant of a study, shows a statistically larger response to faces? While this approach to defining the N170 face effect in an independent localizer may possibly be interesting in some specific cases, we still believe that the outcome of an experiment that relies on this approach would be largely identical to that achieved with a classical approach, that is, merely identifying the channels showing the largest N170 response to faces based on topographical maps and in keeping with the literature to test for an effect of interest.

The Sources of the N170 Face Effect and the Issue of Multiple Components

Is the N170 face effect due to faces eliciting a stronger activation of the sources that generate the N170 to both faces and nonfaces (a *quantitative* effect) or to the addition of one or several specific cortical source(s) for faces (a *qualitative* effect)?

The N170 takes place during a quite long time window (~130–200 ms) at a latency that is well beyond the average onset activation in the primary visual cortex (~50 ms in humans; e.g., Clark et al., 1995; Foxe & Simpson, 2002) and that is compatible with the activation in interlocked time courses of dozens of visual areas in the human brain located on the latero-medial, ventro-dorsal, and antero-posterior axes of the occipital, temporal, and parietal lobes (e.g., Foxe & Simpson, 2002; Vanni et al., 2004). Thus, it is reasonable to assume that the N170/VPP complex on the scalp is due to a configuration of bilateral equivalent dipoles reflecting the vectorial sum of multiple neural sources overlapping in time.

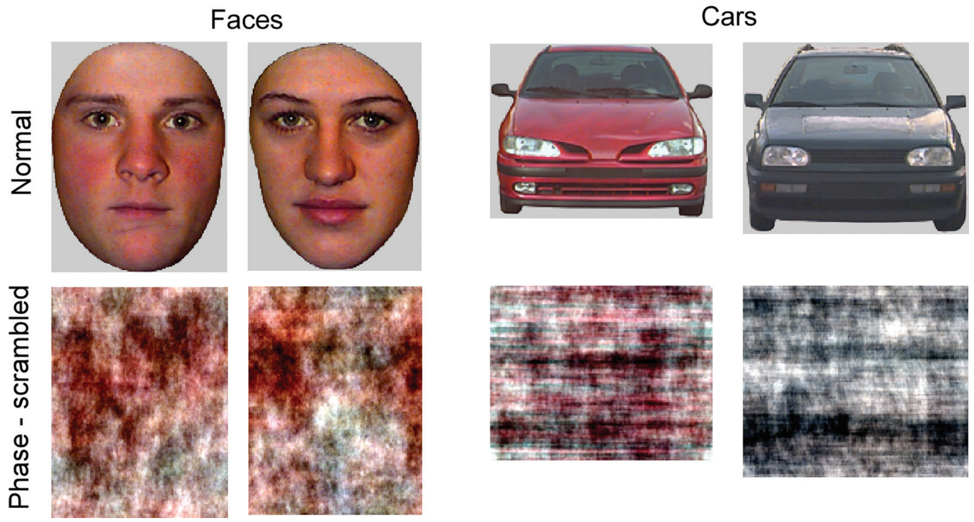

Fig. 5.3. Examples of stimuli that could be used in order to define properly the time window of the N170 face-specific increase in amplitude. Top left, pictures of faces; top right, luminance-matched pictures of a highly familiar category (cars). Pictures of faces and cars differ in terms of color variations and power spectra. Below, these differences can be taken into account by presenting phase-scrambled versions of the above stimuli. The interaction [(Faces–Scrambled faces)–(Cars–Scrambled Cars)] computed pointby point should reveal the differences between faces and nonface stimuli that cannot be accounted for by low-level variations.

Source localization of the N170 to faces using constrained dipolar fit methods (e.g., Scherg & Berg, 1991) reported equivalent bilateral dipole solutions in the lateral occipitotemporal cortex or slightly more medially in the posterior part of the fusiform gyrus (Bötzel et al., 1995; Deffke et al., 2007; Pizzagalli et al., 2002; Rossion et al., 2003a; Schweinberger et al., 2002b; Shibata et al., 2002; Figure 5.3). The M170 has generally been localized in the very same region (Deffke et al., 2007; Halgren et al., 2000; Swithenby et al., 1998; Tanskanen et al., 2005; Tarkainen et al., 2002; Watanabe et al., 1999). This localization would rather correspond to the region of the so-called *occipital face area* (OFA; in BA19) than of the FFA (in BA37) identified in fMRI studies by contrasting pictures of faces and objects (see Haxby et al., 2000; Figure 5.4). However, some studies have also reported a more anterior location of the M170 source in the middle fusiform gyrus, more compatible with an FFA localization (MEG: Linkenkaer-Hansen et al., 1998; Sams et al., 1997; EEG: Mnatsakanian & Tarkka, 2004, as well as two posterior sources in the lingual gyrus; Taylor et al., 2001). Given that the FFA and the OFA are located only about 2 cm apart in the posterior-anterior axis along the ventral visual stream (Figure 5.4), the low

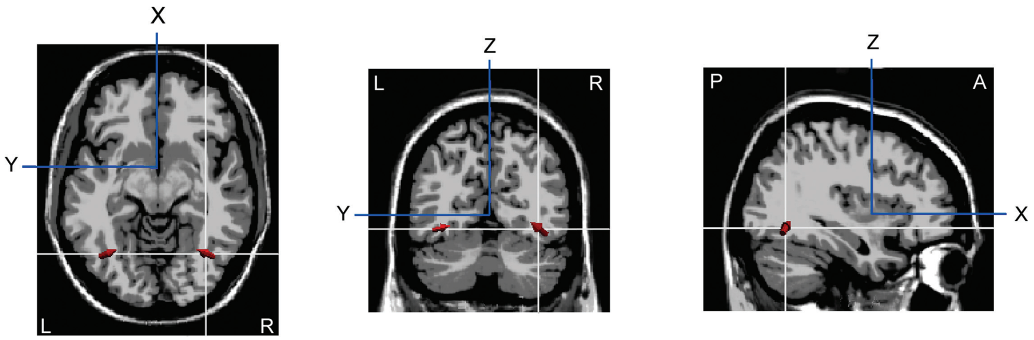

Fig. 5.4. Example of the dipole source localization of the N170 in response to faces (from Rossion et al., 2003) in the posterior fusiform gyrus/lateral occipitotemporal cortex, with their orientation. Many EEG/MEG studies have reported roughly similar localizations of the equivalent dipoles of the N170 (Bötzel et al., 1995; Deffke et al., 2007; Halgren et al., 2000; Pizzagalli et al., 2002; Schweinberger et al., 2002b; Shibata et al., 2002; Swithenby et al., 1998; Tanskanen et al., 2005; Tarkainen et al., 2002; Watanabe et al., 1999). Axes: X = antero-posterior, Y = left-right, Z = dorsal-ventral.

resolution of the EEG source localization, together with the constrains of the dipole fit procedure, may explain this slight difference in source localization.

However, distributed source localization methods without a priori assumptions about the number of sources (e.g., LAURA: Grave de Peralta Menendez et al., 2001; LORETA: Pascual-Marqui et al., 2002) have provided different and contrasting results. Itier and Taylor (2004b) reported a dominant source of the N170 to faces in the posterior part of the superior temporal sulcus (pSTS; see also Watanabe et al., 2003), while Herrmann et al. (2005a) reported main sources in the anterior part of the fusiform gyrus (BA 20), together with multiple activations in a parieto-temporal-occipital network of areas. Henson et al. (2007) used a distributed source localization method with constraints on the number of dipoles and their orientation to test the respective weights of these sources. They also reported dominant sources of the differential M170 for faces and scrambled faces quite anteriorly in the fusiform gyrus, with a strong right hemispheric dominance.

Taken together, these results indicate the presence of multiple cortical sources accounting for the N170 component to faces, with dominant sources in the lateral part of the posterior fusiform gyrus and in the anterior/middle fusiform gyrus. Unfortunately, very few studies have reported the of the sources of the N170 face effect (differential amplitude for faces and objects) or to the N170 in response to objects. Rossion et al. (2003) found equivalent source localization for faces and cars in the posterior fusiform gyrus, but with different strengths and orientations. Itier and Taylor (2004b) reported that faces recruit an additional pSTS source compared to multiple nonface categories, but the sources also varied among nonface categories and were very similar to faces for some categories (e.g., road signs).

To summarize, in light of the current evidence, the question of whether the sources of the N170 to faces and objects differ (i.e., whether the N170 face effect is due to the addition of specific sources or not) is currently unresolved by EEG/MEG studies. In the human brain, fMRI studies have identified several visual areas—the FFA, OFA, and pSTS—that respond more strongly to faces than to other object categories (Haxby et al., 2000; Figure 5.5). However, it is unclear if any of these areas respond *selectively* to faces. High-resolution fMRI has revealed that the FFA is a heterogeneous functional region made up of a high proportion of clusters of the size of several cortical columns, responding selectively to faces, mixed together with clusters responding nonspecifically to any category (Grill-Spector et al., 2006). These face-selective clusters may be the generators of local field potentials such as the intracranial N200 recorded on the surface of the ventral occipitotemporal cortex (Allison et al., 1999) or the much larger P160 response to faces than abstract visual patterns recently reported with intracerebral electrodes implanted in the posterior fusiform gyrus (Barbeau et al., 2008). Similarly, face selectivity is observed in the monkey brain at the level of single neurons (Gross et al., 1972; Perrett et al., 1992) grouped in columns (Wang et al., 1996), which could also be clustered to form larger patches of face selectivity *below* the level of organization of a whole visual area (Tsao et al., 2006).

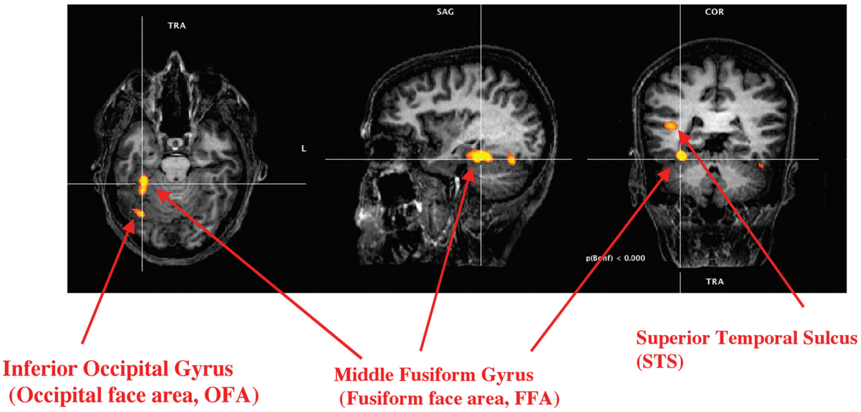

Fig. 5.5. The three functional areas responding more strongly to faces than to nonface visual stimuli in the human brain as identified in fMRI (Haxby et al., 2000). They are illustrated here in the right hemisphere, in a single normal brain, during a functional face localizer contrast (faces vs. objects).

Considering this evidence, the most reasonable account of the N170 face effect on the scalp is that in addition to the contribution of general sources in visual areas responding to object shapes (e.g., the lateral occipital complex), faces recruit a few additional sources in these face areas (i.e., face-selective clusters) between 100 and 200 ms. These sources would contribute heavily to the N170 face effect observed on the scalp.

What Drives the N170 Face Effect?

Does the N170 face effect truly reflect the perception of a face stimulus or rather the low-level properties differing between faces and nonface object categories? In most ERP studies of face processing, low-level properties (e.g., size, luminance, contrast, spatial frequency spectrum) of the categories of stimuli compared, known to influence the amplitude of early visual potentials (see Regan, 1989), are usually not tightly controlled. In general, these factors may also influence the N170 parameters, and thus potentially affect the differential amplitude of this component for faces and nonface object categories. In some studies, however, low-level properties have been controlled as much as possible between faces and the control object category compared (e.g., houses in Rousselet et al., 2005, 2007). In these conditions, the N170 is still much larger in response to faces.

In any case, many observations in the literature indicate that the N170 face effect reflects high-level processes, that is, the *perception* of the stimulus as a face. Two clear illustrations are the larger N170 to the identical two-tone “Mooney” images when they are presented in an upright orientation—and thus are generally perceived as faces—than when they are presented upside down (George et al., 2005; Jeffreys, 1993; Figure 5.6A). In a similar vein, the famous paintings of the sixteenth-century Italian artist Arcimboldo, in which a face is made up of nonface objects (usually organic elements), elicit a clear N170, which decreases substantially when the picture’s orientation is reversed and the face is no longer perceived (Figure 5.6B). In other cases, whenever a stimulus contains enough information (either in the local elements, or in their global configuration, or both) to be interpreted as a face by the visual system, the N170 is large in amplitude. This is true for face photographs obviously, but also for schematic faces, faces with features rearranged, inverted faces, faces cut in half, isolated eyes, faces with contrast inverted, faces without eyes, and so on (see Figure 5.7; e.g., Bentin et al., 1996; Eimer, 1998; George et al., 1996; Itier & Taylor, 2002; Rossion et al., 1999b; Sagiv & Bentin, 2001).

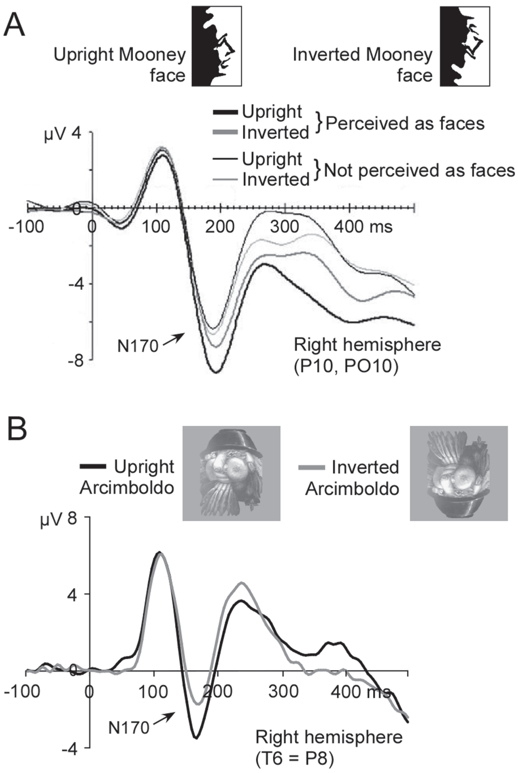

Fig. 5.6. (A) When two-tone (”Mooney”) images are presented upright, they usually lead to the perception of a face stimulus, yielding a larger N170 than when the same pictures are presented inverted and do not lead to the perception of a face (figure adapted from George et al., 2005). (B) The same effect is observed for pictures of the paintings of Giuseppe Arcimboldo (1527–1593), where the face stimulus is perceived as emerging from the organization of nonface features such as fruits and vegetables (Rossion & Jacques, 2008).

However, when a transformation removes most of the diagnostic information used to perceive the stimulus as a face, the N170 is extremely small in amplitude (e.g., an isolated nose or mouth: [Bentin et al., 1996]; superimposed random noise in frequency bands critical for face perception [Tanskanen et al., 2005]). This reduction is also observed when single-stimulus transformations that usually do not reduce the N170 amplitude nevertheless lead to such a reduction when their *combination* affects face perception. For instance, while masking the facial elements through noise *or* inverting the face (i.e., masking the global configuration) may not lead to an N170 amplitude decrease, *combining* the two transformations makes the stimulus difficult to perceive as a face, leading to a substantial N170 amplitude decrease (Schneider et al., 2007).

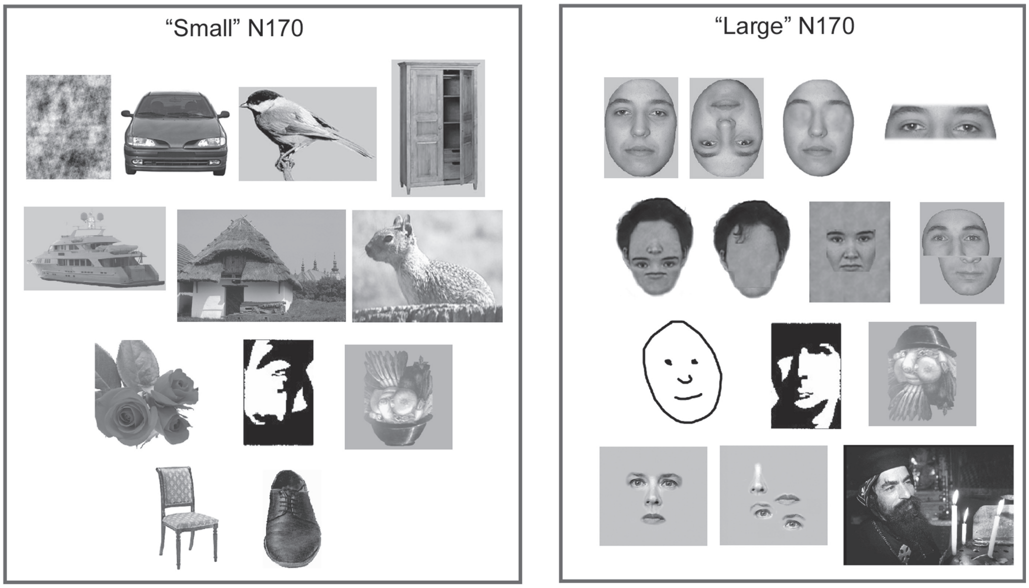

Fig. 5.7. The N170 amplitude is large in response to stimuli that are perceived as a face, across various formats (right), and in comparison to equally complex visual stimuli that can be matched for low-level visual properties (left). When the stimulus is transformed by isolating, masking, or removing facial features, or when the organization of the features is disrupted, the N170 remains large in amplitude or can even be increased as long as the stimulus is perceived as a face. This observation suggests that the N170 onset marks the access to face representations in the human brain. This access is generally slightly delayed in latency (10–20 ms) when the face stimulus is transformed, either at the level of local features (e.g., removing the eyes) or at the level of their first-order organization (e.g., inverting the position of the features).

All of these instances indicate that what drives the increased N170 response is that there must be enough information in the visual stimulus, either as local elements or in their organization, to activate face representations and allow the stimulus to be perceived as a face. Pushing this idea to the limit, Bentin and colleagues also found that the very same simple stimuli, originally not perceived as faces or facial elements, elicited a face-like N170 response only after they conceptually primed study participants' awareness to the physiognomic value of the stimuli (Bentin & Golland, 2002; Bentin et al., 2002). These observations reinforce the view that the N170 face effect reflects the perception of a face and appears to be largely driven by the early activation of neural representations of faces in high-level visual cortex.

Are Early Face Processes Flexible? The N170 and Visual Expertise

Whether neural mechanisms tuned optimally for face perception are strictly modular (domain-specific), or whether they are flexible and potentially recruited for nonface objects following visual expertise, has long been debated (e.g., Diamond & Carey, 1986; Ellis & Young, 1989; Kanwisher, 2000; Tarr & Gauthier, 2000). The N170 face effect is an interesting phenomenon for this debate because it allows testing of the hypothesis that early *perceptual* processes devoted to faces can also be recruited for nonface objects of visual expertise. Supporting this hypothesis, two ERP studies have reported an N170 amplitude increase in bird and dog experts (Tanaka & Curran, 2001) as well as in fingerprint experts (Busey & Vanderkolk, 2005) when they are presented with members of their categories of expertise. One limitation of these studies is that it is unclear whether this amplitude modulation really taps into face processes. This question was addressed directly using an ERP concurrent stimulation paradigm (Jacques & Rossion, 2004). When observers fixate a face stimulus remaining on the screen, the N170 response to another 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). This strong effect is usually taken as evidence for competition between overlapping neural representations and processes. Similarly, when observers fixate a centrally presented object of expertise, the N170 time-locked

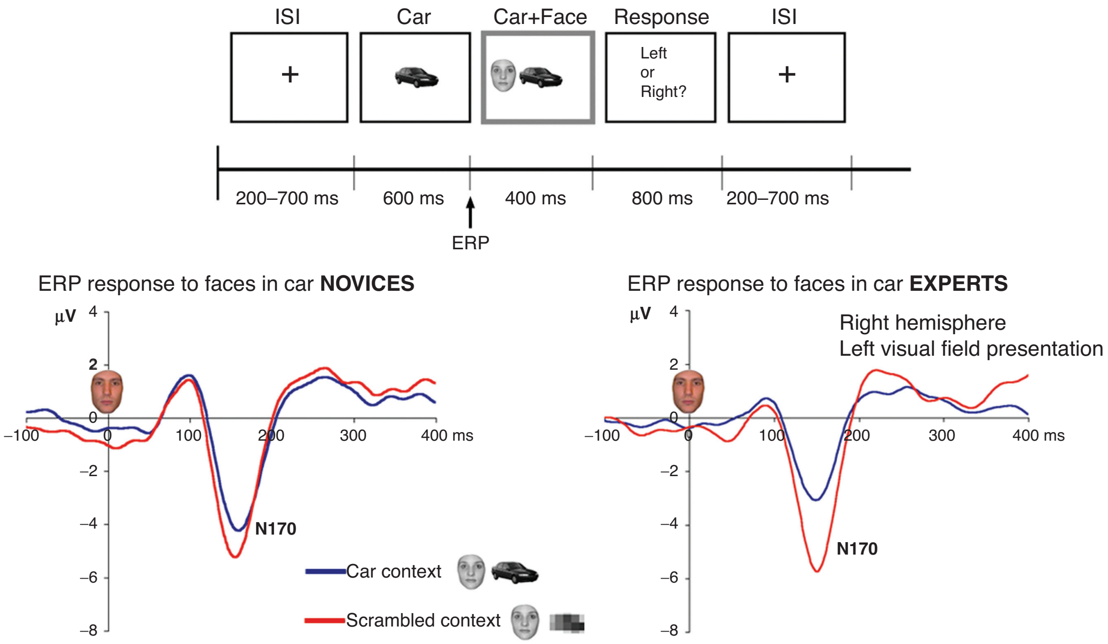

Fig. 5.8. A concurrent stimulation paradigm can be used to show that faces and nonface objects share common perceptual processes during the N170 time window. The ERPs are recorded in response to a face stimulus presented laterally while car experts and car novices fixate either a car or a control stimulus presented in the center of the screen. Relative to novices, the N170 in response to lateralized faces (average of three occipitotemporal electrodes in the right hemisphere) is massively reduced when car experts fixate the picture of a car but not when they fixate the control stimulus. Figure adapted with permission from Rossion et al. (2007).

to a lateralized face stimulus is substantially reduced in amplitude between 130 and 200 ms (Figure 5.8; Rossion et al., 2004, 2007). This sensory competition effect is much larger for experts than for novices and is not found when participants fixate a control nonface stimulus. It is observed for nonface objects learned either in the laboratory (*Greebles*; Rossion et al., 2004) or in real-life conditions (*Cars* in car experts; Rossion et al., 2007). These observations suggest that experts recruit face processes when they fixate nonface objects of expertise, such that the face stimulus that follows can no longer activate the same processes, leading to a reduced N170. Supporting this claim, the degree of visual expertise measured independently through a behavioral task is strongly correlated with the amount of amplitude reduction of the face N170 in the concurrent stimulation paradigm (Rossion et al., 2007). These effects are substantial; they are measured on the N170 elicited by faces, not objects; and they are larger in the right hemisphere in agreement with fMRI localization of visual expertise effects (Gauthier et al., 2000) and the general right hemispheric advantage for processing faces (e.g., Sergent et al., 1992). Furthermore, there is no evidence that these N170 modulations could be due to an increase of central attention to the nonface object of expertise in experts: When manipulated, spatial attention modulates the N170 amplitude to the lateralized face stimulus in an orthogonal (i.e., additive) way to the competition effect and also affects the preceding P1 component (which is unaffected by visual expertise; Jacques & Rossion, 2007a). In summary, by virtue of the excellent temporal resolution offered by ERP recordings and the spatial sampling of the whole system, these observations demonstrate that visual competition between faces and objects of expertise takes place as early as 130 ms in the human brain, during a limited time window, in occipitotemporal areas. However, it remains unclear whether this sensory competition effect results from the recruitment of the exact same neural sources (i.e., clusters of neuronal columns; see the section “The Source of the N170 Face Effect and the Issue of Multiple Components”) for faces and nonface objects of expertise or from increased competitive interactions between distinct populations of cells located in the same area through local lateral inhibitory connections (Allison et al., 2002; Wang et al., 2000). Irrespective of this question, the perceptual mechanisms reflected by the N170 do not appear to be rigidly dedicated to visual stimuli with a facial configuration. They are particularly tuned to faces but remain flexible enough so that they can be partly recruited for some nonface objects following the development of a visual experience at processing these objects.

The N170: A Tool to Disentangle and Carify the Time Course of Face Processes

This section will address the question of what kinds of face processes take place during the N170 time window, and their putative relations to earlier and later face processes as identified in ERPs.

Basic-Level Face Categorization at the Level of the N170

Because of the evidence reviewed above (in the section "What Drives the N170 Face Effect?"), ERP researchers generally acknowledge that the basic-level categorization of the stimulus as a face, or the detection of a face in a visual scene, takes place during the VPP/N170 time window (Bentin et al., 1996; Jeffreys, 1996; Rousselet et al., 2004). This basic-level face categorization stage has been associated with the *structural encoding stage* described in an influential information processing model in the face processing literature (Bruce & Young, 1986). However, as pointed out earlier (Rossion & Gauthier, 2002), this is conceptually incorrect, since the structural encoding stage defined by Bruce and Young (1986) does not refer to a face detection stage, but to the activation of an initial *individual* face representation, common for both familiar and unfamiliar faces, irrespective of the format of presentation of the stimulus (variable in size, viewpoint, etc.).[2] The question of whether individual faces are coded during the time window of the N170 will be addressed below (see the section "The Coding of Individual Face Representations during the N170 Time Window").

Based on the larger N170 amplitude to faces than nonface objects and its correlation with the perception of a face per se (a face percept), it is legitimate to consider that the process of face detection is indeed taking place during the N170 time window. The N170 face effect usually starts at about 130 ms after stimulus onset, although the onset time has rarely been measured precisely (see Rousselet et al., 2005, for an exception) or even discussed. Moreover, the N170 face effect is found for segmented faces or for faces inserted in visual scenes (Rousselet et al., 2004a; 2004b), and appears to be insensitive to large variations of face stimulation in size, position (to some extent), or face viewpoint (Jeffreys, 1996; Rousselet et al., 2005). However, there are two important issues to consider when claiming that the N170 marks the onset of the categorization of the stimulus as a face based on an access to face representations.

DEGRADING FACE STIMULATION DELAYS THE N170

The first issue is that basic-level categorization of a face, or face detection, is partially affected by certain stimulus transformations such as face inversion (Lewis & Edmonds, 2003; 2005; Purcell & Stewart, 1988; Rousselet et al., 2003), which nevertheless do *not* decrease the N170 face effect. In fact, the N170 face effect may even be *larger* following stimulus inversion (Figure 5.9a), because this manipulation

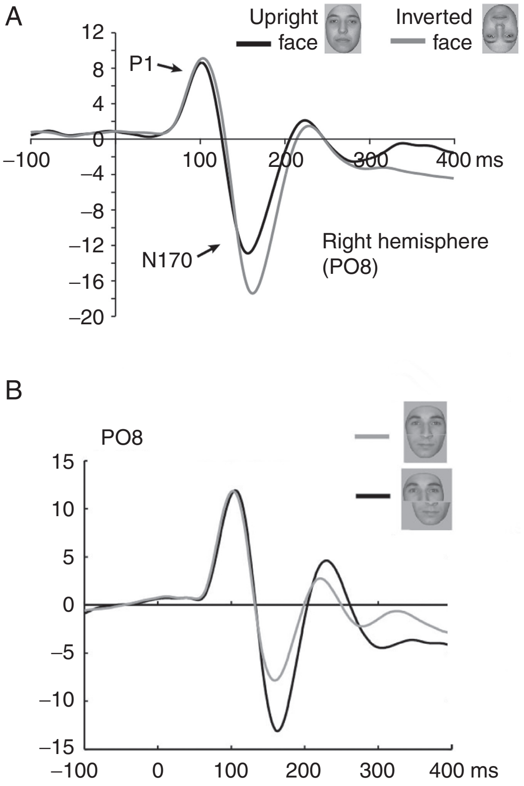

Fig. 5.9. (A) As demonstrated in numerous studies, inversion of a segmented face stimulus, which leads to a massive decrement in individual recognition performance, causes a substantial increase in N170 amplitude (e.g., Eimer, 2000b; Rossion et al., 1999b). Figure adapted from Rossion and Jacques (2008). There are currently no satisfactory accounts of this paradoxical increase in amplitude, which is at odds with the slight reduction of neural activity for inverted faces as recorded in fMRI (e.g., Kanwisher et al., 1998), single neurons (Perrett et al., 1998), or local field potentials recorded on the cortical surface (Allison et al., 1999). (B) Breaking the face stimulus into two parts, even slightly, also leads to an amplitude increase in the N170 (Letourneau & Mitchell 2008; ERP waveforms of this figure from Jacques & Rossion, unpublished data).

increases the amplitude of the N170 to faces while leaving the N170 to nonface objects of identical or similar amplitude (e.g., Rossion et al., 2000). The same paradoxical N170 increase is found for other manipulations that may affect the categorization of the stimulus as a face, such as isolating the eyes (e.g., Bentin et al., 1996; Taylor et al., 2001), changing the features' positions (George et al., 1996), inverting the contrast of the face (Itier & Taylor, 2002), or laterally offsetting the bottom part of the face (see Figure 5.9b; Letourneau & Mitchell, 2008). Moreover, as noted above, the N170 remains very large for faces without eyes, for instance (Eimer, 1998; Itier et al., 2007) or when a small amount of visual noise is added to the image (e.g., Jemel et al., 2003c; Schneider et al., 2007). How can these observations be reconciled with the idea that the N170 largely reflects the initial activation of face representations associated with the categorization of the stimulus as a face? One critical element to consider here is that all these transformations of the face stimulus, which increase the N170 amplitude or leave it unaffected, do not *prevent* the stimulus from being categorized as a face. As mentioned above (in the section "What Drives the N170 Face Effect?"), if sufficient elements are present, either as features or as a first-order configuration, so that the stimulus is perceived as a face, the N170 will be large in amplitude. However, removing or degrading some elements of the face will generally *slow down* the activation of the representation, an effect that is reflected in the delay (10–20 ms) of the N170 following inversion (e.g., Bentin et al., 1996; Rossion et al., 1999b, 2000; Figure 5.9) as well as for the above-mentioned stimulus transformations (e.g., Bentin et al., 1996; Eimer, 1998; George et al., 1996; Itier & Taylor, 2002; Itier et al., 2007). One possibility is thus that the delay of the N170 due to stimulus transformations such as inversion merely reflects a delay in the activation of face representations or a slower accumulation of evidence at the level of the neuronal population coding for faces (see Perrett et al., 1998). Recent evidence suggests in fact that both mechanisms may be at play, because the latency delay measured at the N170 peak for inverted faces is correlated with variations of the ERP signal as early as 120–130 ms (N170 onset) but is maximal at the N170 peak (Jacques & Rossion, 2007b).

In summary, despite stimulus transformations that slow down face detection, whenever a face representation is activated, it is associated with a large N170 response.

EARLY FACE DETECTION (P1/M1) IS BASED ON LOW-LEVEL VISUAL FEATURES

A second issue to consider is whether the time window of the N170 is too late to reflect the basic categorization of a face stimulus, a process that is extremely fast. Indeed, both ERP and forced-choice saccadic eye movement studies indicate that categorization of animal or human faces in pictures of visual scenes, for instance, can take place within 110–150 ms following stimulus onset, *including the perceptual decision* (Crouzet, Kirchner, & Thorpe, 2010; Thorpe et al., 1996, VanRullen & Thorpe, 2001). How can this finding be reconciled with the idea that the N170 marks the onset of basic-level categorization of faces? One possibility is that a stimulus may be detected in a visual scene and categorized as a face above chance level before the onset of the N170, but that this fast categorization is not based on the activation of face representations. Rather, it could be based on an accumulation of evidence from low-level cues that are statistically more frequently associated with faces (e.g., roundness, specific color distribution in the visual scene, local contrast, distribution of energy in different frequency bands) and can lead to fast basic-level face categorization.

Along these lines, several studies have reported a larger P1 (or M1 in MEG) in response to faces than to objects (e.g., Eimer, 1998, 2000a; Goffaux et al., 2003; Herrmann et al., 2005a, 2005b; Itier & Taylor, 2004a; Liu et al., 2002) at electrodes near the medial occipital pole at about 100 ms following stimulus onset. This P1/M1 face effect is not consistently observed (e.g., Boutsen et al., 2006; Rossion et al., 2003; Rousselet et al., 2005, 2007) and is not as large as the N170 face effect (e.g., Goffaux et al., 2003; Itier & Taylor, 2004a; Liu et al., 2002; see Figure 5.10). It has sometimes been associated in the literature with high-level face processes, such as basic-level face categorization (Herrmann et al., 2005b), the perception of facial parts (Liu et al., 2002), or holistic/configural face processing (Halit et al., 2000; Latinus & Taylor, 2005).

However, several elements suggest that the P1/M1 face effect does not reflect face perception per se, but rather is related to differences between faces and nonface stimuli in terms of intrinsic low-level visual information (see also Rossion & Caharel, in press). First, the visual P1/M1 is an early component, peaking at around 100 ms following stimulus onset, and thought to originate mainly from striate and lateral extrastriate visual areas (Clark et al., 1995;

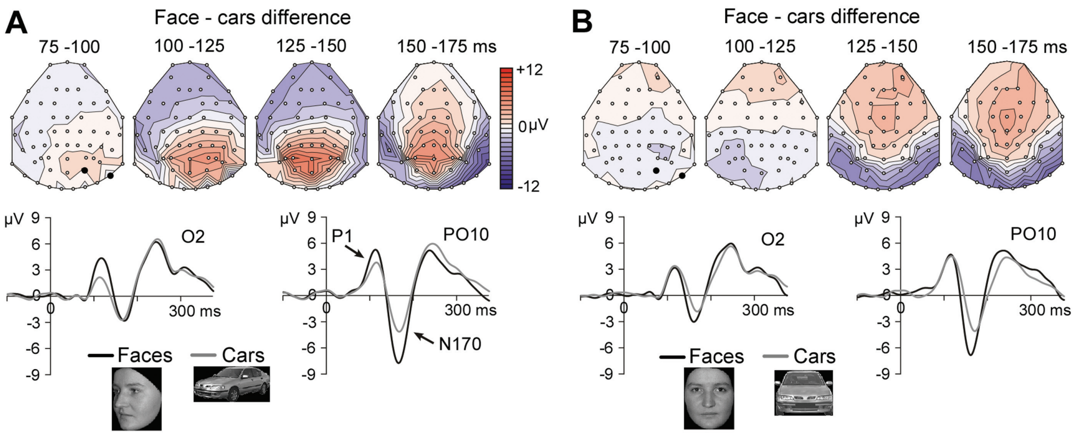

Fig. 5.10. (A) Grand average ERP to three-quarter views of faces and cars. The upper row shows scalp topographies of the difference between faces and cars (from 75 to 175 ms after stimulus onset). The lower row depicts raw ERPs at two posterior electrodes (location indicated in black on the left scalp topography). Note the large amplitude difference at the level of the P1 and N170 components both on ERP waveforms and on scalp topographies. (B) Grand average ERP to front views of faces and cars. Details are identical to those in (A). When front-view symmetrical stimuli are presented, ERPs to faces and cars no longer differ at the level of the P1 component, while the N170 is still much larger for faces. This is visible on ERP waveforms and scalp topographies. The fact that the N170 (but not the P1) is larger for faces irrespective of the viewpoint indicates that this effect is robust even for symmetrical full-front images of the two categories (as for Figure 5.1, unpublished data). Figure adapted with permission from Rossion and Jacques (2008).

Di Russo et al., 2002; Halgren et al., 2000; Tanskanen et al., 2005; Tarkiainen et al., 2002), even though some studies have reported a contribution of the posterior fusiform gyrus (Hermann et al., 2005b; Liu & Ioannides, 2006). P1 amplitude is known to be sensitive to many low-level visual features such as luminance, color, contrast, or spatial frequencies of the stimulus (see Regan, 1989). Supporting this view, the early M1 difference between photographs of faces and other categories can be reversed in amplitude (Halgren et al., 2000) and can be canceled when surface information (color and texture) of the face stimuli is removed (while the M170 face effect resists these low-level transformations). In the same vein, studies in which the face and object stimuli are well controlled for low-level features do not report P1 face effects (e.g., Rousselet et al., 2005). More intriguingly, while the N170 face effect appears to generalize across views of the stimuli, the P1 face effect may disappear when symmetrical full-front pictures of faces and cars are presented, indicating that it is not always reliable (Rossion & Jacques, 2008; Figure 5.10).

Second, given the early onset latency of the P1 (~80 ms) compared to the mean onset latency of face-selective neurons (100 ms in the monkey brain e.g., [Kiani et al., 2005], probably slightly later in the human brain, see Schroeder et al., 2004), it is unlikely that this P1/M1 face effect reflects the activation of facial representations. Similarly, intracranial recordings have so far demonstrated earlier face-preferential or face-specific responses clearly after 100 ms, that is, N200s in the ventral occipitotemporal cortex and lateral middle temporal gyrus (Allison et al., 1999) and P160 in the posterior fusiform gyrus (Barbeau et al., 2008; see also Halgren et al., 1994). Third and finally, strong support for the dissociation between a low-level and a high-level origin of the P1 and N170 face effects, respectively, has been reported by studies varying parametrically the amount of visual noise or the noise spatial frequency added to a face image. While the P1/M1 is not correlated with the amount of face information in the image manipulated parametrically through random noise, the N170/M170 amplitude increases with visibility of the face (Jemel et al., 2003c; Tarkiainen et al., 2002). Most interestingly, an elegant MEG experiment (Tanskanen et al., 2005) dissociated the M1 and M170 effects by masking face stimuli with narrow-band spatial frequency noise. When the noise was presented in the frequency bands optimal for face perception (11–16 cycles per image), the face could not be perceived adequately, but the occipital M1 was maximal in amplitude. In contrast, the M1 was minimal and the M170 was maximal at the lowest and highest noise spatial frequencies, in parallel with the clear perception of the face (Figure 5.11). These results underline the two

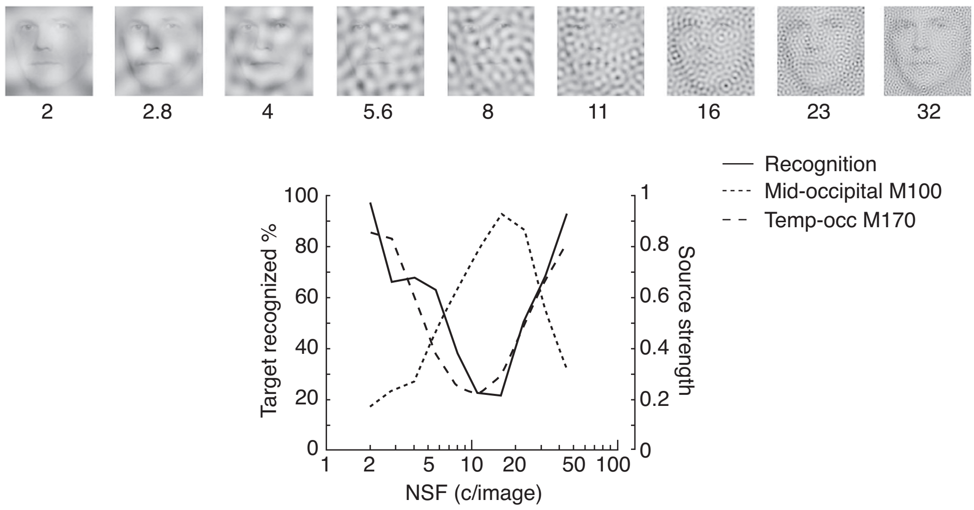

Fig. 5.11. By adding noise at different frequency bands on face stimuli (top row), Tanskanen and collaborators (2005) showed a dissociation between the M100 (M1) and M170 amplitude response properties. The M170 is larger when the noise is in the highest and lowest spatial frequency bands, that is, when it does not affect the perception of the stimulus as a face (see the full line). In contrast, the M100 is larger when the energy is higher in the mid-frequency bands, masking the perception of the stimulus as a face. This shows not only that the M170 amplitude is a function of the perception of the stimulus as a face, but also that the face-sensitivity effects found on the M100 may be due to the specific power spectrum of face stimuli, with more information in the mid-frequency bands. Figure adapted with permission from Tanskanen et al. (2005).

important points of this section. First, the M170 response is sensitive to the visibility of a face and is closely related to face perception. Second, the M1 is not sensitive to the perception of a face per se, but its response is largest to the middle spatial frequencies that are critical for face perception. This strongly suggests that at the level of the M1, the face effect reported by some studies is meaningful and reflects the early accumulation of evidence to categorize the stimulus as a face. However, this categorization is based on low-level visual information, such as the spatial frequency spectrum or color of the stimuli, rather than on the activation of face representations per se (see also Rossion & Caharel, in press for recent direct evidence). Therefore, the N170 time window appears to offer the most reliable time frame to investigate the nature of face perceptual mechanisms in the human brain, even if earlier face sensitivity can be observed.

The Coding of Individual Face Representations during the N170 Time Window

While detecting a face in the visual scene is a complex and biologically relevant task, in most circumstances our face processing system has to go beyond this initial categorization and extract an individual face representation in order to be able to determine if that person has been seen previously. How fast does the system extract a representation that is detailed enough to individualize a face?

In humans, this question has been mostly investigated by measuring the ERP responses to repeated individual faces. The rationale behind repetition studies is that the time point at which the ERP signal diverges for repeated and unrepeated faces indicates the speed at which the system is sensitive to the differences among individual faces.

A series of studies have used a *delayed repetition* paradigm that includes a phase during which a number of faces are learned (either only visually or by association with a name and/or brief semantic information such as an occupation; e.g., Curran & Hancock, 2007; Joyce & Kutas, 2005; Paller et al., 2000; Yovel & Paller, 2004). Other studies have compared the ERP response to the first presentation of faces with the ERP response to the same faces presented in a subsequent block of trials (e.g., Henson et al., 2003; Schweinberger et al., 2002a; Tanaka et al., 2006). All of these studies thus include a variable number of intervening face stimuli between the first and subsequent face presentations. Notably, *none* of these delayed face repetition studies has reported a modulation of the N170 when comparing repeated to unrepeated faces. Rather, the most robust finding in these studies is that repeated faces elicit a larger N400 potential compared to unrepeated/new faces in a time window ranging from around 300 to 500 ms. This effect has been termed the *ERP repetition effect* or the *old/new ERP effect* (e.g., see Paller et al., 2000).

From these observations, one might conclude that the coding of individual faces occurs no sooner than 300–400 ms after stimulus onset, that is, about 200–300 ms after the stimulus has been categorized as a face (i.e., at the onset of the N170, around 130 ms). However, this conclusion is at odds with the speed at which individual faces can be discriminated behaviorally (Figure 5.12), as well as the known temporal dynamics of face information encoding by face-selective neurons in the nonhuman primate inferotemporal cortex. These neurons have an average onset latency of about 100 ms and accumulate information about both global face category and face identity simultaneously (Tovee & Rolls, 1995), with information about individual faces being significantly represented in the neurons' responses not more than 40–50 ms after presentation of information about the global category (Matsumoto et al., 2005; Sugase et al., 1999).

This discrepancy suggests that the use of a delayed repetition paradigm in ERPs may not provide reliable information about how sensory/early visual representations are modulated by repetition. That is, these representations may not hold the trace of a previously presented stimulus for a prolonged time interval.

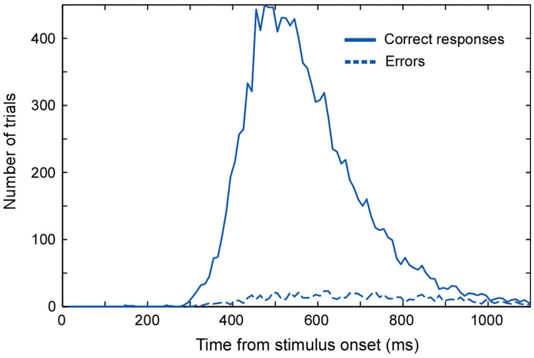

Fig. 5.12. Distribution of response times in an individual face discrimination same/different task (Jacques & Rossion, 2007b) in which faces were presented at 12 orientations in the picture plane (0–330°). The histograms represent the distribution of correct and incorrect responses pooled across all face orientations. The number of trials in successive 10 ms time bins is plotted as a function of time from stimulus onset. Note that the earliest correct responses start at around 300 ms after stimulus onset. If we consider that a minimum of 100 ms is needed to generate a motor command (see VanRullen & Thorpe, 2001), this response time distribution points to a coding of individual faces before 200 ms.

When using *immediate* face repetition, some studies found that the N170 is slightly reduced in response to a face preceded by the same individual face compared to a face preceded by a different face (e.g., Campanella et al., 2000; Guillaume & Tibergien, 2001; Heisz et al., 2006; Itier & Taylor, 2002; Jemel et al., 2003a, 2005). However, other studies did not find any N170 amplitude difference between repeated and unrepeated faces (e.g., Huddy et al., 2003; Jemel et al., 2003b; Mnatsakanian & Tarkka, 2004; Schweinberger et al., 1995, 2002b, 2004). The factors accounting for this discrepancy between studies are difficult to identify. Moreover, a common criticism of these effects is that they may reflect general repetition effects that could also be due to image-based elements and not to the repetition of an individual face per se.

Recently, two ERP paradigms were used to address these limitations and investigate systematically the time course of individual face coding. First, in a long adaptation paradigm (~3000 ms duration for the adapter) with a short interstimulus interval (100–300 ms) between the adapting face and the target face, the N170 amplitude was substantially reduced when the test face was of the same identity as the adapting face, starting at around 160 ms (Jacques et al., 2007; Figure 5.13). This effect was found despite the use of different photographs and a change of size between the adapter and the target face (Jacques et al., 2007). Importantly, when the identical face stimuli were presented upside down (Figure 5.13), the difference between same and different faces was not found on the N170 but was delayed by about 30 ms (i.e., starting at ~190 ms). Moreover, a recent ERP adaptation experiment with similar timing parameters (i.e., presentation duration and interstimulus interval) indicates that the adaptation effect to face identity on the N170 is robust enough to generalize at least partly across a 30 degrees viewpoint change between adapting and target faces (Caharel et al., 2009a). These observations further rule out an interpretation of this N170 individual face adaptation effect as being due to simple physical differences rather than to perceived differences between individual faces. This strong and replicable effect of visual adaptation found for individual faces on the N170 (Caharel et al., 2009a; 2009b; Jacques et al., 2007; Jacques & Rossion, 2009) stands in contrast with inconsistent effects found in previous face identity repetition studies. Several factors may account for this discrepancy,

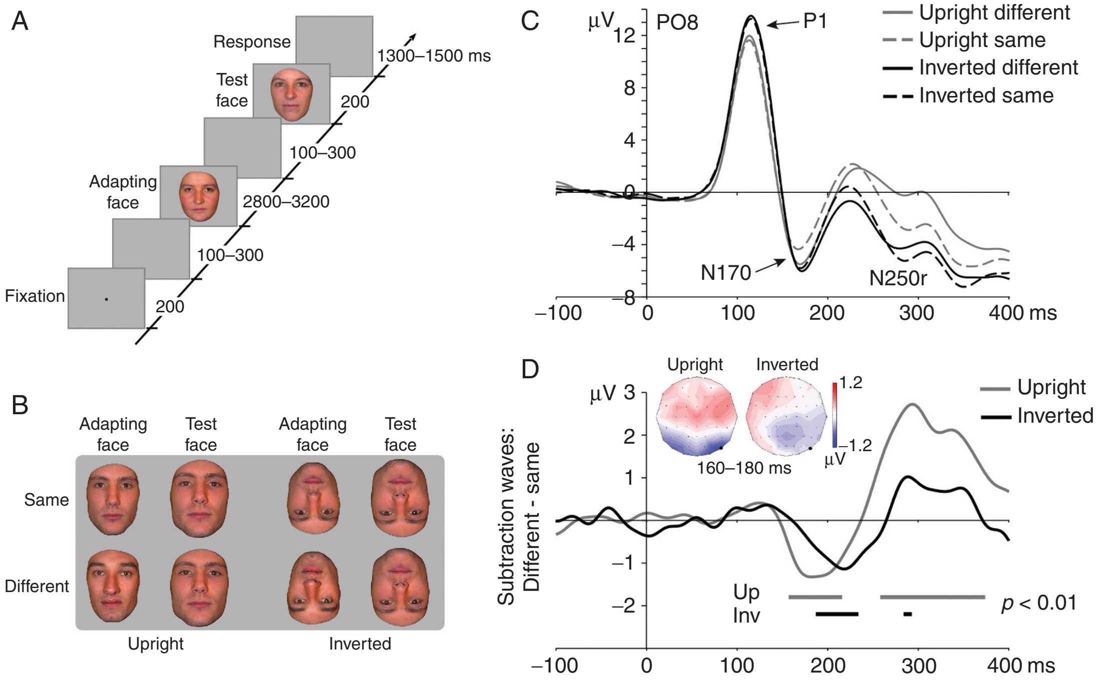

Fig. 5.13. (A) An individual face adaptation ERP paradigm (Jacques et al., 2007) with a long duration of the adaptor and a short interstimulus interval was used during a delayed matching task. (B) The four conditions of the experiment, crossing adaptation (adapting and test faces = same or different) with orientation (upright inverted). (C) The ERP response to the test face. There is a strong interaction between adaptation and orientation starting at the N170 level, with a reduction of amplitude for the upright same faces only. (D) Subtraction waveforms (different–same faces) on electrode PO8 and topographical maps, showing that the identity adaptation effect starts at around 160 ms for upright faces but takes place about 30 ms later (after the N170 component) for the inverted faces and is much weaker. Significant differences ($p < .01$) between waveforms recorded in the same versus different conditions are indicated as horizontal gray bars for upright faces (Up) and black bars for inverted faces (Inv). Note also the large effect of identity adaptation following the N170 at the level of the N250 component (see, e.g., Schweinberger et al., 2004). Figure adapted with permission from Jacques et al. (2007).

in particular the longer duration of the first stimulus (adapter), which is necessary to elicit behavioral face adaptation effects (see, e.g., Leopold et al., 2005) and has been also used successfully in an ERP-adaptation study at the level of the face category (Kovacs et al., 2006). Another element to consider is the short interstimulus interval between the adapter and the target face (~200 ms) used by Jacques, Rossion and colleagues in their studies compared to the longer intervals (usually >1 s) used in previous immediate repetition studies.

Second, converging evidence of individual face coding at the level of the N170 is found when a continuous face identity reversal paradigm is used (Jacques & Rossion, 2006). Here, instead of recording the N170 in response to a "flashed" face (i.e., presented after a blank screen period), the ERP is recorded to an individual face that follows immediately the presentation of another face (i.e., pattern-reversal stimulation, or face identity reversal here). In these conditions of identity reversal stimulation (~2 Hz), early visual components preceding the N170 are abolished and a "pure" N170 response can be isolated. This stimulation mode allows measurement of the ERP response reflecting the difference between two individual faces (Figure 5.14). Using morphed stimuli in a categorical face perception design, it was found that the isolated N170 response was larger when the two faces reversing identity were located on different sides of the identity boundary, compared to when they were located on the same side of the identity boundary (Jacques & Rossion, 2006), again ruling out a low-level visual account of these observations.

To summarize, both ERP adaptation and face identity reversal stimulation indicate that the system can discriminate between individual face representations as early as 160 ms during the late N170 time window. These observations suggest that the N170 should not only be described as a face detection

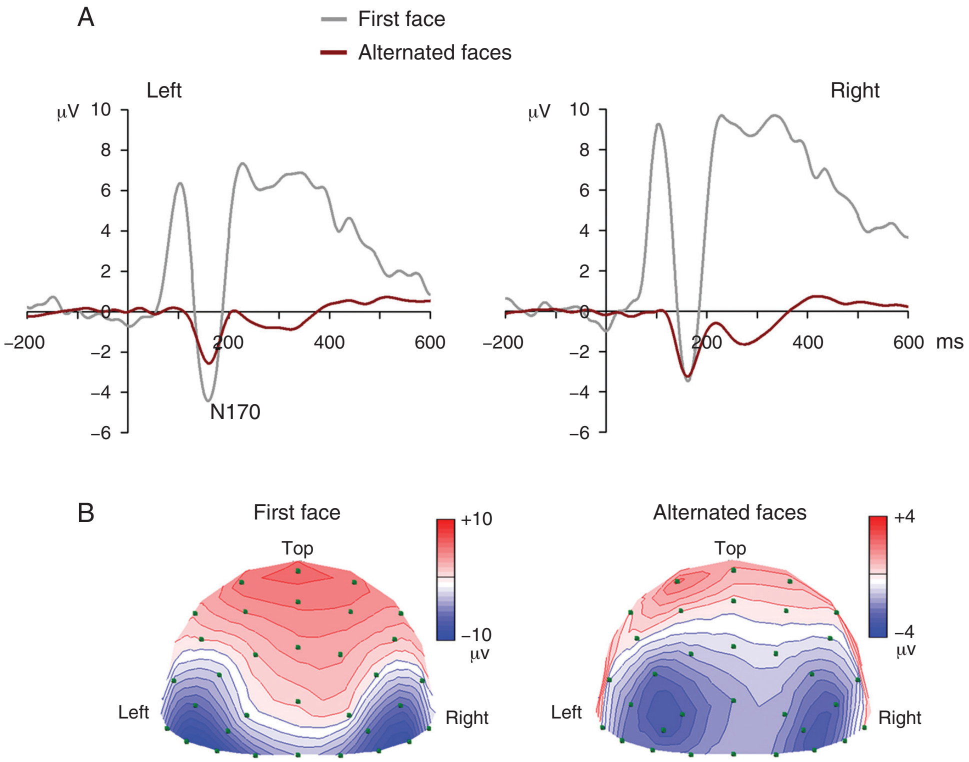

Fig. 5.14. (A) An ERP to the first face of a block of trials (preceded by a blank screen) superimposed on the ERP in response to the face identity reversal (electrodes PO7 and PO8). Note that the onset of the response to a face identity reversal is at the N170 level (130 ms), that is, the P1 component is no longer present. (B) The scalp topographies (back view of the head) depict the distribution of the ERP response at 160 ms following the onset of the first face of each block (left) or the alternated face (right). Figure adapted with permission from Jacques and Rossion (2006).

stage. Rather, it is a time window during which multiple face processes take place, including both face detection *and* the coding of individual faces. Or, to put it differently, once a face representation has been activated, it can be rapidly refined into an individual representation *within* the N170 time window. Of course, this is not to say that the whole process of the individual face representation is completed during the N170 time window. For instance, an additional individual face repetition effect is usually observed starting at around 220–250 ms after stimulus onset. This repetition effect generally arises in the form of a more negative ERP for repeated compared to unrepeated faces around 250 ms over temporal scalp regions, and has accordingly been termed the *N250* or *N250r* (e.g., Begleiter et al., 1995; Schweinberger et al., 1995; Tanaka et al., 2006). Thus, even though the processing of an individual face starts during the N170 time window, information continues to be further accumulated during the later time window, as reflected by the repetition effects occurring at later time points (see Jacques et al., 2007, for a time-point-by-time-point analysis of individual face repetition effects).

Are Long-Term Face Representations Activated during the N170 Time Window?

When are long-term stored representations of individual faces activated? Most studies have found that the N170 does not discriminate between unfamiliar faces and famous faces (e.g., politicians, celebrities; Bentin & Deouell, 2000; Eimer, 2000a; Henson et al., 2003; Jemel et al., 2003a, 2003b, 2005; Schweinberger et al., 2002a) or learned faces (Rossion et al, 1999a). In contrast, famous faces usually elicit an enhanced N400 component (i.e., between 300 and 500 ms; Bentin & Deouell, 2000; Eimer, 2000a; Jemel et al., 2003a, 2003b) over central or frontocentral electrodes and an increased positivity between 500 and 700 ms over central or centroparietal sites (Bentin & Deouell, 2000; Eimer, 2000a; Henson et al., 2003) when compared with unfamiliar faces.

However, a series of recent studies have found a larger N170 for *personally* familiar faces (the subject's own face, mother's face, friends' faces) or very famous faces compared to unknown faces (Caharel et al., 2002, 2006). Similarly, an MEG study (Kloth et al., 2006), found a larger N170 to personally familiar faces (lecturers and fellow university students) compared to unfamiliar faces. The larger amplitude for familiar faces starts at around the peak of the N170 (160–170 ms) and is maximal in the descending slope of the N170, similar to the timing of individual face adaptation effects on the N170 (Jacques et al., 2007). Furthermore, the N170 difference between familiar and unfamiliar faces is no longer present for faces presented upside down (Caharel et al., 2006), in agreement with the behavioral face inversion effect and with N170 adaptation findings (Jacques et al., 2007).

Part of the discrepancy between the studies that found or did not find an effect of face familiarity on the N170 is due to the comparison of unfamiliar with *personally* familiar faces in the latter group (Caharel et al., 2002, 2006; Kloth et al., 2006), whereas the former used famous faces, for which there may be large individual differences in the degree of familiarity of the participants with each face. Specifically, the visual coding of personally familiar faces, which would be associated with more robust representations (Tong & Nakayama, 1999), may be facilitated by the extensive visual experience that observers have with these faces, hence yielding a differential N170 response when compared to unfamiliar faces (Caharel et al., 2002).

Alternatively, these familiarity effects on the N170 might reflect a top-down modulation from stored face representations, as suggested by the finding of a strong familiarity effect on the N170 (comparing famous to unfamiliar faces) only when faces had been previously presented (i.e., a priming paradigm; Jemel et al., 2003b). More precisely, the (prolonged) activation of stored robust face representations, due either to the large number of repetitions of familiar faces (Caharel et al., 2002) or to the use of semantically related familiar faces (e.g., friends, family members, fellow students; Caharel et al., 2002, 2006; Kloth et al., 2006), may have biased the visual encoding of individual faces taking place at the N170. It is therefore currently unclear whether this N170 familiarity effect arises due to face familiarity per se (i.e., the information about face familiarity is contained in the individual face representations extracted during the N170) or to top-down modulations.

The N170 and Other Face Categorizations

This review has largely focused on how the N170 reflects the coding of a face in order to detect faces and process their identity. However, faces are extremely complex stimuli, carrying a large number of cues that are important for social interactions. From a face, we are able to extract information allowing us to recognize the facial expression and the mood of the person, and to categorize the face's sex, infer its race, or infer its apparent age (Bruce & Young, 1998). Furthermore, primates can also detect rapidly and automatically the direction of gaze to determine where the person is looking (see, e.g., Emery, 2000). The extraction of the cues leading to these categorizations of the face stimulus is notoriously fast and efficient, yet little is known about its time course. Most EEG/MEG studies that have addressed the issue of the speed and time course of face categorization besides identity processing have contrasted the perception of different stimuli (e.g., male and female faces, faces with different expressions, directed and averted gaze). With the exception of studies contrasting different eye-gaze directions (e.g., Conty et al., 2007; Taylor et al., 2001), the majority of these studies have failed to report modulations at the level of the N170 (for expression, see, e.g., Eimer & Holmes, 2002; for age and gender, see, e.g., Mouchetang-Rostaing & Giard, 2003; for race, see, e.g., Caldara et al., 2004). Some studies have reported amplitude modulations of the N170 for different facial expressions, in particular a larger N170 to fearful faces than neutral faces (e.g., Batty & Taylor, 2003; Blau et al., 2007). However, it is unclear if these effects are due to low-level features (e.g., increased contrast between dark and white areas of the face in fearful expressions) or to the differentiation of facial expressions per se. Other modulations of the N170 with facial expression are largely inconsistent among studies. Our view on this issue is in line with the evidence reviewed above: Since the N170 marks the early access to both global and fine facial information, there is no reason to believe that the extraction of cues to categorize rapidly and efficiently a face according to its gender, age, race, or facial expression would not also take place predominantly within that time window. However, there is no reason to expect that the raw N170 amplitude, which reflects the global activation of the system, would differ reliably in response to various face stimuli (e.g., two faces with different expressions) that activate largely overlapping populations of neurons. Rather, the sensitivity of the component to the differential information contained in these stimuli needs to be assessed through ERP adaptation paradigms (i.e., changing expression between adapter and target) or continuous changes of expression, for instance (as performed in some eye gaze studies; e.g., Conty et al., 2007; Watanabe et al., 2001). Future ERP/ERMF research using such paradigms will then have to disentangle these different effects in both time and space in order to clarify the exact time course of face categorization processes.

Summary, Questions to Clarify, and Future Directions

Summary

The N170 is a visual component that is much larger in response to pictures of faces than to any kind of comparable visual stimulation (i.e., the N170 face effect) and has accordingly been studied as a marker of perceptual face processes (see the section "The Early ERP Studies of Face Processing and the N170 Face Effect"). As indicated in the introduction, there are currently more than 100 published ERP/ERMF studies focusing on the N170/M170 component, and an extensive review of these studies, their findings, and their implications was clearly beyond the scope of this chapter. In concentrating on answering basic questions regarding the N170 in this chapter, we had to omit a number of important issues, such as whether the component can be modulated by spatial and selective attention (Eimer, 2000c; Jacques & Rossion, 2007a), how it is affected in clinical populations (prosopagnosia, autism, etc.; e.g., Dawson et al., 2005; Eimer & McCarthy, 1999), what its developmental course is (de Haan et al., 2002; Kuefner et al., 2010; Taylor et al., 1999), and clever experiments using the particular tuning of the N170 to faces to understand the mechanisms of visual working memory maintenance, for instance (Sreenivasan et al., 2007). The interest in these studies directly depends first on how the basic issues that were addressed in this chapter are clarified and understood among the scientific community of N170 researchers.

Here, in summary, we have seen that the N170 corresponds to a time-locked increase of EEG amplitude (see the section "The N170: Time-Locked Increase in EMG Amplitude Rather Than Intertrial Phase Realignment") and originates most likely from multiple cortical sources, with dominant bilateral sources in the posterior fusiform/lateral occipitotemporal complex as well as the middle fusiform gyrus (see the section "The Sources of the N170 Face Effect and the Issue of Multiple Components"). The N170 is larger in the right hemisphere in response to faces. Even though the N170 face effect appears to reflect the important contribution of processes taking place in visual areas activated preferentially for face stimuli, these processes remain plastic enough in the adult visual system to be recruited partly for nonface objects following extensive expertise training (see the section "Are Early Face Processes Flexible?").

There is widespread evidence that the N170 onset (~130 ms) reflects the earliest activation of face representations in the occipitotemporal cortex: The N170 is large in amplitude as long as the stimulus is perceived as a face, even if either the local features or their global configuration is disrupted (see the section "What Drives the N170 Face Effect?"). As long as the stimulus remains interpretable as a face, the N170 presents a large amplitude. However, it can be delayed when the access to face representations is slowed down following manipulations such as removing diagnostic features, presenting the features in isolation, or breaking the first-order face organization through scrambling or inversion (see the section "Basic-Level Face Categorization at the Level of the N170"). Contrary to this categorization of the stimulus as a face based on the nature of the features and their configuration, earlier face-sensitive effects at the level of the P1 appear to reflect largely low-level visual differences between faces and nonface objects such as their differential power spectra or color distribution (see Rossion & Caharel, in press). Future studies should go beyond a mere debate between ERP components by performing point-by-point correlation between electrophysiological and behavioral responses. When performing such analyses (e.g., Jacques & Rossion, 2007b; Philiastides & Sajda, 2006), the exact time point at which the effects of stimulus and task manipulations arise can be identified. Such analyses usually reveal significant effects *after* the P1 component in the downward slope of the N170 (e.g., Jacques & Rossion, 2007b; Rousselet et al., 2007).

The first access to individual face representations takes place during the late N170 time window, in agreement with the speed of individual face coding in the monkey brain (see the section "The Coding of Individual Face Representations during the N170 Time Window"). However, the question of whether personally familiar face representations are already activated at that latency requires stronger evidence (see the section "Are Long-Term Face Representations Activated during the N170 Time Window?").

Although the processing of an individual face starts during the N170 time window, further information continues to be accumulated during the later time window, as reflected by repetition effects occurring at later time points (e.g., the N250 component; see, e.g., Schweinberger et al., 1995; 2002b). It is our view that other finer-level face categorizations of the stimulus (e.g., expression, gender) are also performed during the N170 time window at various latencies (see the section "The N170 and Other Face Categorizations"), but decisive evidence requires the use of more sensitive paradigms than the comparison of different stimuli presented in isolation.

The Road Ahead: Caveats and Recommendations for N170 Research

Even though we know that both basic-level (coarse) and fine face categorization processes take place during the N170 time window, the *nature* of the face representations and the time course of their activations during the N170 time window remain largely unclear. For instance, one may ask whether certain facial features or properties have more weight in the face representations or are activated earlier than others. More generally, during the N170 time window, are faces processed through the extraction of local facial parts that are then integrated into a global representation (i.e;? *local to global*) or rather from an initial coarse global face picture to a finer-grained representation (i.e., *global to local*)?

The majority of studies that have addressed this question of the nature of face representations and its dynamics have proceeded by comparing the N170 amplitude in response to single face stimuli that are transformed or degraded. This is done either in a hypothesis-driven way in most studies (e.g., revealing, masking, or modifying only certain predetermined features of the face; e.g., Bentin et al., 1996; Eimer, 1998; Itier et al., 2007) or in an unbiased sampling of small portions of the stimulus (e.g., Schyns et al., 2003). The nature of the information coded is then inferred from the modulation of N170 amplitude with the stimulation, much as the response properties of single neurons of the monkey infero-temporal cortex are inferred from their spiking rate following degradation of complex visual stimuli (e.g., Tanaka, 1996). The ERP studies adopting this approach have mainly confirmed the well-known finding that the eyes are a dominant feature of the face (e.g., Haig, 1985), eliciting a conspicuous N170 even when presented in isolation (Bentin et al., 1996). This large N170 to isolated eyes has been sometimes interpreted as evidence that there is a distinct source devoted to the eyes of the face contributing heavily to the N170 (e.g., Bentin et al., 1996; Itier et al., 2007) or that the representation of the face during the N170 reflects mainly the local information about the eyes (Schyns et al., 2003). Yet, this interpretation is problematic because the N170 amplitude is large in response to a face defined only through its first-order configuration, even without any eyes or other features (e.g., the Arcimboldo paintings; see the section "What Drives the N170 Face Effect?"; Figure 5.6). Moreover, as long as the stimulus is still perceived as a face, removing the eyes from a face photograph does not attenuate the N170 amplitude at all (Eimer, 1998; Itier et al., 2007). Hence, one cannot infer from the larger N170 to isolated eyes that the eyes are perceptually processed in a distinct population of neurons or that they represent a critical feature to elicit the N170.

In a similar vein, the interpretation of an *earlier* representation of the local eye region than any other features based on the N170 amplitude during the presentation of randomly selected facial information through small apertures (Schyns et al., 2003, 2007) could be mistaken. Indeed, this effect may be simply due to a *quantitative* difference, that is, the fact that the N170 amplitude is large in response to isolated eyes but not to other isolated internal features (Bentin et al., 1996). However, when a full-face stimulus is presented, there is currently no evidence that information on the eyes is processed before information on the other features of the face. This example illustrates how the raw N170 amplitude in response to a single stimulus, while being informative about the faceness of that stimulus, cannot be directly taken as reflecting the nature of the representation at that latency. One reason for this limitation is that, as we have seen (see the section "What Drives the N170 Face Effect"?), once there is enough evidence in the stimulus to activate a face representation (a process that can be facilitated by the viewer's expectations), a large N170 is evoked. The eyes may have more weight in the activation of the representation of a face, in particular when the stimulus is not segmented or masked by noise (Paras et al., 2007), but this does not mean that the eyes of the face are processed in a separate neural source, that they are critical, or that their representation is activated first in time when features are presented altogether. Moreover, the N170 amplitude is certainly *not proportional* to the strength of activation of the representation, being in fact larger to degraded or transformed face stimuli

(Figure 5.9). A second reason for this limitation is that contrary to the response of a single neuron, the N170 amplitude reflects the *global* contribution of multiple cortical sources that are activated in interlocked time courses and can compensate for or counteract each other. For these reasons, directly inferring the nature of the coding from the raw N170 amplitude to single stimuli that reveal partial information of a face appears to be misleading.

As noted earlier in this review, and similarly to what is currently being done in many fMRI studies (Grill-Spector & Malach, 2001), a more adequate and sensitive approach to characterizing the nature of the face representations during the N170 time window may be to rely on modulations of the N170 amplitude following face adaptation (*ERP adaptation* within the face domain; e.g., Ewbank et al., 2008; Harris & Nakayama, 2007; Caharel et al., 2009b; Jacques et al., 2007; Figure 5.13) or reversal of certain features of the face in a continuous stimulation paradigm (see Jacques & Rossion, 2006; Figure 5.14). Here the interest is no longer in clarifying what the component reflects but rather in using it as a *tool* to clarify the nature of early face representations and processes. For instance, presenting a face stimulus after an adapter and modifying separately or in combination various properties, such as the overall shape of the face, its pigmentation, particular facial features, distances between features, and so on, should potentially reveal *if*, *how strongly*, and *when* exactly these cues are coded during the N170 time window (or later) (for a recent example see Caharel et al., 2009b). Another advantage of this approach is that it isolates specific effects during the processing of *whole faces* rather than degraded or transformed stimuli. Given that the literature reviewed in this chapter clearly indicates that the N170 is a critical time window for investigating human face processing, an approach that treats the N170 component as a tool to investigate the nature of face processes and their time course during natural stimulation of whole faces appears to us to be one of the most promising in this field.

Notes

1 The C1 reverses polarity with the presentation of the stimulus in the upper/lower visual field (associated with a negative/positive polarity, respectively) due to reversal of the orientation of the sources with respect to the calcarine sulcus (see, e.g., Clark et al., 1995; but see Ales et al., 2010).

2 According to Bruce and Young (1986, p. 307), the structural encoding stage is considered as a level "which capture those aspects of the structure of a face essential to distinguish it from other faces" and thus supposedly reflects individual face coding.

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