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Chapter 17

The Face-Sensitive N170 Component of the Event-Related Brain Potential

Martin Eimer

Faces are perhaps the most important object category in visual perception, as faces of conspecifics frequently convey behaviourally, socially, and emotionally relevant information that is critical for the adaptive control of action. Given this undisputed significance of faces, it is not surprising that the study of human face processing has long been one of the most active research areas in visual cognition. In recent years, numerous new insights into the mechanisms and neural processes that underlie our ability to perceive and recognize faces have come from studies that have investigated face processing with neuroscientific methods. Functional brain imaging studies have identified the fusiform face area (FFA; Kanwisher et al., 1997), the right lateral occipital face area (OFA; Gauthier et al., 2000b), and the superior temporal sulcus (Hoffman and Haxby, 2000) as regions that are specifically involved in the processing of faces (see Haxby et al., 2000, for a review of the neural network involved in human face perception; Haxby and Gobbini, Chapter 6, this volume). Electrophysiological evidence for face-specific brain processes has been obtained through intracranial recordings (Allison et al., 1999), as well as in many studies using event-related brain potentials (ERPs). These ERP studies have uncovered several components that are linked to different stages in face perception, face recognition, and the processing of emotional facial expression (e.g. Eimer, 2000c; Eimer and Holmes, 2007).

The earliest, most prominent, and by far the most widely studied face-sensitive ERP component is the N170. When compared to different categories of non-face objects, human faces consistently elicit a larger negative-going ERP component at occipitotemporal electrodes. The presence of an N170 component in response to faces has been demonstrated in two early ERP investigations of human face perception (Bentin et al., 1996; Bötzel et al., 1995), and the N170 has since featured prominently in face perception research. There are currently more than 200 published studies that have used this component to investigate different aspects of face processing in the human brain. More recently, an “M170” component with response properties that are very similar but perhaps not identical to the N170 has been identified in experiments that used magnetoencephalographic (MEG) measures to study face processing (e.g. Halgren et al., 2000; Harris and Nakayama, 2008).

The purpose of this chapter is to introduce the N170 component to readers who may not be intimately familiar with the details of ERP methodology and interpretation, and to provide a brief review of some important research questions that have been addressed by employing the N170 as an electrophysiological marker of face processing. The first section will discuss basic properties of the N170 component, its neural basis, as well as some methodological issues that need to be kept in mind when using this component to study face-specific processes, and when evaluating the results from previous N170 experiments. In the next section, a recent methodological challenge to the claim that the N170 reliably reflects face-specific brain processes (Thierry et al., 2007a) will be evaluated and rejected. The following two sections review research that has employed the N170 component to investigate two central and interrelated issues in face processing. First, the relative roles of configural versus feature-based processes in face perception will be addressed. The fourth session discusses the domain-specificity or generality of face processing, as well as the possible role of expertise. Finally, some avenues for future research will be outlined.

C17.S1 The N170 component—measurement, cortical generators, and relationship with the "vertex positive potential" (VPP)

Before reviewing recent research that has used the N170 component to study different aspects of face processing, it is essential to clarify what precisely is claimed when this component is described as face-selective. This claim does emphatically *not* imply that this component is triggered exclusively in response to faces. The N170 belongs to the family of visually evoked (or "exogenous") N1 components that are elicited over visual brain areas in response to most types of visual stimuli regardless of their category. The N170 has acquired its status as a face-sensitive component because ERP amplitudes elicited at occipitotemporal electrodes between 140 ms and 200 ms after stimulus onset are virtually always larger in response to faces than in response to non-face objects. It is this *amplitude difference* between faces and non-face stimuli with its characteristic scalp topography (see below) that is thought to reflect the activation of face-selective brain areas. Given that research on the N170 is essentially based on such amplitude differences, the common description of the N170 as a *face-specific* ERP component is potentially misleading, since it incorrectly implies that this component is triggered exclusively in response to faces. The N170 response should be more accurately characterized as *face-sensitive*, and this label will be used in this chapter.

The fact that the N170 is a visual evoked ERP component implies that, similar to earlier visual components such as the P1, it is strongly affected by variations in the low-level perceptual attributes of visual stimuli, such as their size, contrast, luminance, retinal eccentricity, or spatial frequency. Therefore, for any comparison of N170 amplitude differences between face and non-face objects to be meaningful, it is essential to ensure that such low-level visual features do not differ systematically across the visual object categories of interest. A careful control of physical stimulus properties is extremely important for any ERP experiment that employs naturalistic stimuli such as photographs of faces and other visual objects. Even though enhanced occipitotemporal negativities in the N170 time range to faces as compared to pictures of non-face objects such as houses, hands, cars, household objects or animals have been consistently observed in several hundred ERP studies, it has recently been argued that this apparent face-sensitivity of the N170 does in fact result from the uncontrolled variation of low-level visual stimulus attributes (Thierry et al., 2007a). This specific challenge will be discussed in detail in the next section.

Figure 17.1 (top panel) shows a typical pattern of ERP responses to face versus non-face objects that was obtained in the author's lab in response to centrally presented faces and houses. ERPs are shown separately for left and right occipitotemporal electrodes P7 and P8 and for the vertex electrode Cz. An enhanced negativity to faces is clearly visible at both lateral posterior electrodes in the N170 time range, and this differential effect is more pronounced over the right hemisphere. Figure 17.1 also makes clear that in addition to the N170, an enhanced positivity to faces as compared to houses was elicited at electrode Cz. This "vertex positive potential" (VPP) usually accompanies the N170 component, and is elicited in the same time range. In fact, early ERP studies of face processing (Bötzel and Grüsser, 1989; Jeffreys, 1989) identified the VPP as an electrophysiological correlate of face processing well before the N170 component became the major focus of ERP research.

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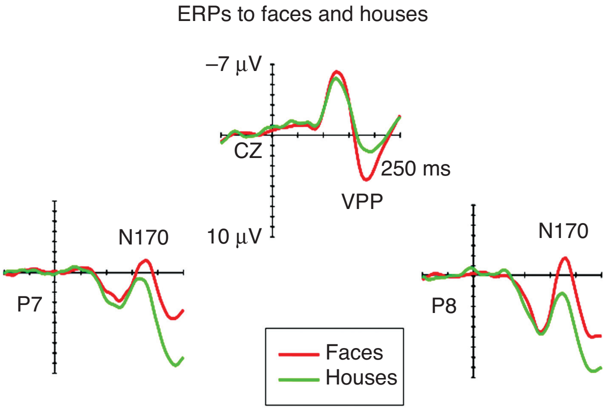
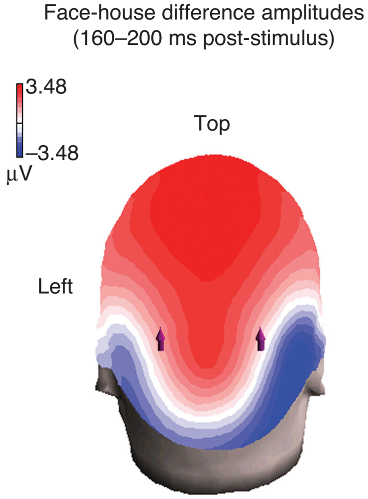


ERPs to faces and houses



Face-house difference amplitudes (160–200 ms post-stimulus)

Fig. 17.1 Top panel: Grand-averaged ERP waveforms in response to faces and houses presented at fixation, shown for the first 250 ms after stimulus onset. Negative amplitudes are plotted upward. ERPs at midline electrode Cz are characterized by an enhanced positivity to faces relative to houses. This "vertex positive potential" (VPP) has its maximum at about 180 ms after stimulus onset. At lateral occipitotemporal electrodes (P7, P8), the VPP is accompanied by an enhanced negativity for faces relative to houses (N170), which here also peaks at about 180 ms post-stimulus. Bottom panel: Scalp topography of ERP differences between houses and faces, measured for the N170 time window (160–200 ms after stimulus onset). Enhanced negativity for faces versus houses is shown in blue, enhanced positivity for faces versus houses in red. The face-sensitive N170 (marked in blue) is maximal over lateral occipitotemporal areas, and disappears rapidly at more medial and dorsal posterior electrode sites. The face-sensitive VPP (marked in red) is maximal at the vertex, but extends into more posterior and inferior areas. N170 and VPP are likely to reflect the activity of the same underlying neural generator processes. A plausible location for bilateral symmetric dipoles in lateral temporal cortex is indicated here by the two forward-pointing arrows. C17.F1

There has been considerable debate as to whether the N170 and the VPP reflect the same underlying neural processes, or whether they represent the activity of two functionally distinct electrical sources. Although some studies have reported small latency differences between N170 and VPP (e.g. Bentin et al., 1996) or a differential sensitivity of these components to peripherally presented face versus non-face objects (Eimer, 2000a), there is now substantial evidence that the response properties of the N170 and VPP are closely associated across a range of stimulus and task manipulations (Jemel et al., 2003; Itier and Taylor, 2002; Joyce and Rossion, 2005), which suggests that they represent the same underlying face-sensitive brain processes. This is also intuitively plausible when examining the topography of these two components: Figure 17.1 (bottom panel) shows an ERP scalp distribution map obtained by subtracting ERPs to houses from ERPs to faces in the N170 time range (160–200 ms poststimulus). The lateral posterior negativity (N170) and centrally distributed positivity (VPP) shown here can both be accounted for by a pair of symmetrical dipoles in lateral temporal cortex that point towards the vertex. Joyce and Rossion (2005) have recently demonstrated that relative amplitude differences observed between the N170 and the VPP in earlier studies are largely due to the choice of reference electrodes during EEG recording: with mastoid reference, N170 amplitudes were small and VPP amplitudes were maximal, while the reverse pattern of results was observed when a nose reference was used instead. Joyce and Rossion (2005) recommend a common average reference as the most suitable method for recording face-sensitive ERP components with minimal distortion.

Although the scalp topography of face-sensitive brain responses in the N170 time range, as shown in Figure 17.1 (bottom panel), strongly suggests bilateral posterior temporal cortical generator processes, source localization studies of the N170 and its magnetic counterpart (M170) have yielded somewhat inconclusive results. Some of these discrepancies between studies may be linked to the different methods used to estimate the cortical sources of these components. Studies that employed dipole fitting methods to explain the pattern of electrical activity observed on the scalp surface have suggested bilateral occipitotemporal cortex and the posterior fusiform gyrus as likely origins of the N170 (e.g. Bötzel et al., 1995; Rossion et al., 2003) and M170 (e.g. Halgren et al., 2000; Deffke et al., 2007). These posterior regions overlap more closely with the localization of the occipital face area (OFA; Gauthier et al., 2000b) than with the fusiform face area (FFA; Kanwisher et al., 1997), as described in functional imaging studies (but see Sams et al., 1997 for evidence that more anterior fusiform regions including the FFA might also contribute to the M170). Source localization studies that have estimated the cortical origins of scalp-recorded ERP topographies not by dipole fitting, but by computing distributed brain activation patterns have obtained different results, with sources for the N170/M170 localized in the posterior superior temporal sulcus (STS; Itier and Taylor, 2004; Watanabe et al., 2003), or right fusiform gyrus (e.g. Henson et al., 2007). Such discrepancies between source localization studies are partly due to the limited spatial resolution of EEG and MEG, and to the fact that different methods for estimating the locus of neural generator processes were used. However, they also suggest that N170 and M170 components are not linked to a single source, but are instead generated by multiple simultaneously active face-sensitive brain processes that are primarily located in lateral occipitotemporal areas. One important focus for future research on the N170 component will be the study of possible functional dissociations between these different cortical generator processes and their respective contributions to face processing.

C17.S2 Is the face-sensitivity of the N170 an artifact of uncontrolled interstimulus perceptual variance?

In the past 10 years, the face-sensitive N170 component has been employed in a large number of ERP studies to investigate the time course, neural basis, and functional organization of face

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perception. This research has by no means resolved all questions about the interpretation of the N170 and its links to the specific mechanisms that are involved in face processing. Some of these issues will be discussed in the following two sections. However, the basic consensus is that the N170 component is a valid electrophysiological reflection of face-sensitive brain processes. A recent article (Thierry et al., 2007a) has challenged this assumption. According to Thierry and colleagues, the core finding of numerous studies that N170 amplitudes are larger in response to faces than for any other object category is based on a critical, and hitherto unrecognized methodological artifact: in all of these experiments, enhanced N170 components for faces relative to non-face objects were observed because the face images that were used in these studies were physically more similar to each other than were the images within non-face object categories.

Thierry et al. (2007a) introduced the concept of "interstimulus perceptual variance" (ISPV) to describe the physical similarity between tokens within a given object category. ISPV is low when all tokens share a basic structure (e.g. when images of individual faces all show the same frontal view, are all presented at fixation, and are identical in size). ISPV is high when individual tokens differ substantially in terms of their basic physical attributes (e.g. when images of non-face objects are presented from different viewpoints, or vary in their size or location). According to Thierry et al. (2007a), the apparent face-sensitivity of the N170 component is an artifact of inadequate stimulus control, and specifically of systematic ISPV differences between faces and other stimulus categories, because in typical N170 experiments, ISPV is generally low for faces, and higher for non-face objects. High ISPV increases the variability of ERP peak latencies across single trials, and this latency jitter results in a systematic reduction of ERP peaks in averaged waveforms. Reduced N170 amplitudes for non-face objects as compared to faces would thus be the consequence of systematic between-category differences in ISPV. Once ISPV is controlled, the face-sensitivity of the N170 would be abolished. Thierry et al. (2007a) support this provocative claim by presenting data from two experiments where they manipulated the ISPV of faces and non-face objects (cars or butterflies). Larger N170 components for faces were found only when the ISPV of faces was low and the ISPV of non-faces was high. In contrast, when the ISPV level was the same for faces and non-faces, no N170 amplitude differences were observed.

Not surprisingly, these results, and in particular the conclusions that were drawn by Thierry and colleagues, have elicited a hostile and extremely critical response from the N170 community (Bentin et al., 2007; Rossion and Jacques, 2008). Can it really be the case that all previous studies that have used the N170 component as a critical marker of face processing are now invalidated due to the presence of an unrecognized methodological confound? Fortunately for researchers that have used or intend to use the N170 to study face processing, any such reports on the demise of this face-sensitive component are definitely premature. In fact, the arguments put forward by Thierry and colleagues have already been conclusively refuted (see Rossion and Jacques, 2008, for detailed arguments). However, the fact that these arguments were originally published in a highly visible multidisciplinary journal may still lead researchers who are not familiar with the intricacies of ERP methodology to assume that the N170 component cannot provide any valid insights into the brain mechanisms that underlie face processing. It will therefore be useful to briefly summarize the case against Thierry et al. (2007a) in this chapter.

As described in the previous section, the N170 is a visual evoked ERP component, and is therefore not only sensitive to faces, but is also affected by variations of low-level visual features. Because of this fact, absolute N170 amplitudes can vary substantially as a result of differences in visual stimulus parameters such as luminance, spatial frequency, contrast, symmetry, and retinal eccentricity. It is therefore not very surprising that ISPV may be another low-level variable that has the potential to affect N170 amplitudes. However, Thierry et al. (2007a) do not just claim that ISVP can modulate the size of the N170, but instead, and much more controversially, that uncontrolled ISPV differences across object categories can account for all previously reported N170 amplitude differences between faces and non-face stimuli, and that the face-sensitivity of the N170 disappears when ISPV is held constant.

The case against Thierry and colleagues (2007a) includes two main lines of argument: on the one hand, there appear to be substantial methodological flaws in their own experiments, specifically with respect to the measurement of the N170, which may have obscured the real face-sensitivity of this component. On the other hand, and even more importantly, the claim by Thierry et al. (2007a) that previous N170 studies failed to control for ISPV is simply wrong, and their conclusion that the N170 is no longer face-sensitive when ISPV is held constant is therefore plainly inconsistent with existing data.

With respect to the internal methodological problems of the experiments reported by Thierry et al. (2007a), it is likely that they may have missed face-sensitive N170 modulations because their choice of electrodes used to measure N170 amplitudes was inappropriate. As can be seen in Figure 17.1, N170 amplitude enhancements to faces relative to non-face objects have a distinct lateral occipitotemporal distribution. This face-sensitive effect is usually maximal at lateral posterior electrodes such as P7 and P8, and its amplitude declines rapidly at more medial occipital electrodes. Likewise, face-specific N170 modulations are rarely observed at more dorsal occipitoparietal electrode sites. If anything, these electrodes are more likely to pick up the posterior part of the VPP component (the positive-going counterpart of the N170, see Figure 17.1). In spite of these well-known facts about N170 scalp distribution patterns, Thierry and colleagues chose to quantify N170 amplitudes by including medial occipital and parietal electrodes. It is therefore not very surprising that they observed generally very small N170 amplitudes, and no systematic differences between faces and non-faces. This diagnosis is further supported by inspecting the ERP waveforms from more appropriate occipitotemporal electrodes that were provided by Thierry and colleagues (2007b) in their response to a critique of their original paper by Bentin et al. (2007). Here, the N170 was indeed larger for faces than for cars, at least when ISPV was high for both categories, which appears to directly contradict their original claims.

Not only do the N170 data that Thierry and colleagues have put forward to support their controversial conclusions suffer from an inappropriate choice of electrode sites, but their claims also do not stand up in the light of existing studies of the N170 component. First of all, it is simply not correct that previous experiments on the N170 have not considered ISPV as a possible confounding factor. In fact, in the vast majority of these studies, including those conducted by the author of this review, great care has been taken to equate the size, location, and viewpoint for images of face and non-face objects, in order to minimize any differences between object categories in terms of the low-level physical attributes of individual stimuli (see Rousselet et al., 2008 for a recent example). There is therefore no reason to assume that ISPV was generally much higher for non-face images than for faces in all previous N170 experiments. Although ISPV has usually not been explicitly measured for different stimulus categories, closer scrutiny of existing studies reveal that ISVP is not a critical factor for N170 amplitudes in general, and for the face-sensitivity of this component in particular. Bentin et al. (2007) present a re-analysis of the N170 results obtained by Rossion et al. (2000) in response to faces, houses, cars, and novel visual objects ("greebles"). ISPV values for each of these categories were estimated by computing the pixel-by-pixel correlation between all images within the same category. N170 amplitudes were maximal in response to faces, and were basically unrelated to differences in ISPV between object categories. Perhaps most tellingly, N170 amplitudes were much larger for faces than for houses, in spite of the fact that ISPV was minimal for houses (i.e. individual houses were more similar to each other than were the items in the other three categories), and substantially larger for faces. In another study (Goffaux et al., 2003), substantially larger N170 amplitudes were observed to faces than to cars, in spite of the fact that ISVP was virtually identical across these two stimulus categories. In addition to these two examples, similar dissociations between ISPV and N170 amplitudes could be easily demonstrated on the basis of numerous other existing studies (see Bentin et al., 2007, and Rossion and Jacques, 2008, for more examples). Further strong evidence against the claim that the apparent face-sensitivity of the N170 is due to a confound with ISPV comes from numerous studies that have shown that the N170 is modulated by face inversion. These studies will be reviewed in the next section section. Because stimulus inversion leaves ISPV unaffected, such N170 face inversion effects cannot be due to an uncontrolled variation of this factor.

To summarize, the strong claims put forward by Thierry et al. (2007a) can be safely refuted not only on the basis of internal problems related to the measurement of the N170, but most compellingly because of the conclusive evidence from many other studies which demonstrates that the face-sensitivity of the N170 component bears virtually no relationship to variations in ISVP across stimulus categories. The systematic methodological artifact that might threaten to invalidate all previous research on the N170 does simply not exist. Nevertheless, the contribution by Thierry and colleagues may still serve as an important reminder that careful control of low-level visual stimulus attributes remains an essential aspect of research in visual cognition, and in particular in experiments that measure brain responses to natural images, such as photographs of faces and non-face objects. If stimulus control is not sufficiently rigid, the unrecognized variance of elementary perceptual features between image categories could indeed lead to mistaken claims about category-specific processing.

The N170 as a marker for the structural encoding and configural processing of faces

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The face-sensitivity of the N170 strongly suggests that this component is linked to cortical processes that are involved in the category-selective processing of faces. Several studies have demonstrated that the N170 is unaffected by the familiarity of faces (e.g. Bentin and Deouell, 2000; Eimer 2000c; but see Caharel et al., 2002 for diverging results), indicating that this component is associated with face processing stages that precede the identification of individual faces. It has therefore been suggested (e.g. Eimer, 2000d; Sagiv and Bentin, 2001) that the N170 is an electrophysiological marker for the perceptual structural encoding of faces that takes place prior to face recognition. The existence of face-specific structural encoding was originally postulated in the influential face processing model by Bruce and Young (1986) as the stage where visual representations of the features of individual faces are generated. Even though the N170 is typically unaffected by the long-term familiarity of faces, it does show systematic repetition effects for individual unfamiliar faces: N170 amplitudes are reduced when the same face is presented twice in rapid succession, relative to trials where the second face image shows a different individual (e.g. Jemel et al., 2005). Such identity-dependent N170 adaptation effect can even be observed when the two successively presented faces differ in their viewpoint (Caharel et al., 2009). These observations are fully in line with the hypothesis that the N170 is linked to the structural encoding of individual faces. In addition, the N170 typically shows little sensitivity to the emotional expression of a face (Eimer and Holmes, 2002; Eimer et al., 2003; but see Batty and Taylor, 2003 for different results). The observation that facial expression modulates ERPs at anterior electrodes in the 140–200 ms post-stimulus latency window, whereas the face-sensitive N170 that emerges in the same time window at lateral posterior electrodes is not affected by emotional expression (see Eimer and Holmes, 2002, 2007) is in line with the assumption of Bruce and Young (1986) that structural encoding and the detection of the emotional expression of faces represent two parallel and independent stages of face processing (see also Chapter 22 by Calder, this volume, for a more detailed and critical discussion of this assumption).

The question of how the structural encoding of faces, as reflected by the N170 component, differs from the perceptual processing of other types of objects is still a subject of considerable debate. One key difference between face and object processing is that that inversion has a much larger negative effect on the perception and recognition of faces than on the perception and recognition of non-face objects This "face inversion effect" (e.g. Yin, 1969) is usually explained by assuming that inversion specifically disrupts the processing of configural information, and that this type of information is much more important for the perception and recognition of faces than for the processing of other types of visual objects (for more details, see McKone and Robbins, Chapter 9; Tanaka and Gordon, Chapter 10, this volume). While some authors (e.g. Tanaka and Farah, 1993) postulate that faces are analyzed in a holistic fashion, others (Leder and Bruce, 2000) assume that relational information (e.g. the spatial configuration of specific face parts) is the key aspect in the configural processing of faces (see Rossion, 2008; and Rossion and Gauthier, 2002 for more detailed discussions of the difference between the holistic and relational interpretation of face-specific configural processing). Still others (e.g. Valentine, 1988) have claimed that inversion does not primarily affect the perception of faces, but instead their post-perceptual encoding in memory, which is less efficient when faces are inverted.

The N170 has played an important part in this debate, as this component is highly sensitive to face inversion. One of the most reliable and replicable features of the N170 is that it is delayed by about 10 ms in response to inverted as compared to upright faces (Bentin et al., 1996; Eimer, 2000b; Itier et al., 2006, 2007; Rossion et al., 2000; Sagiv and Bentin, 2001). A similar effect of face inversion on the latency of the face-sensitive VPP (the positive counterpart of the N170 at midline electrodes, see the first section in this chapter) was already reported by Jeffreys (1989). Although some small inversion-induced N170 latency delays have recently also been observed for some non-face objects (Itier et al., 2006), this latency shift is generally much more pronounced and consistent for inverted faces. The delay of the N170 in response to inverted faces has been attributed to the disruption of configural face processing that is caused when prototypical spatial relationships between face parts are altered as a result of face inversion. The fact that face inversion systematically affects an early visually evoked component such as the N170 provides conclusive evidence for a perceptual locus of the face inversion effect, and against the view that this effect is primarily generated during the encoding of inverted faces in memory (Valentine, 1988).

However, face inversion does not just result in a delay of the N170 component, but is also typically reflected by an enhancement of N170 amplitudes (Bentin et al., 1996; Eimer, 2000b; Rossion et al., 2000; Sagiv and Bentin, 2001). The fact that the N170 is larger for inverted than for upright faces is often considered as puzzling: if face inversion disrupts configural processing, an ERP marker such as the N170 that is supposed to be sensitive to this type of processing should be attenuated rather than enhanced in response to inverted faces. Several explanations have been put forward to account for the paradoxical increase in N170 amplitude for inverted faces. According to one hypothesis (Itier et al., 2007), the inversion-induced enhancement of N170 amplitudes is linked to the additional recruitment of eye-sensitive cells by inverted faces. These authors assume that the N170 component is primarily generated in STS, which includes both face-selective and eye-selective neurons. Upright faces activate only face-selective, but not eye-selective cells, because the latter are assumed to be inhibited when presented in the context of an upright face (see also Perrett et al., 1988). The disruption of prototypical face configurations induced by face inversion releases eye-sensitive neurons from context-induced inhibition. In line with their account, Itier et al. (2007) demonstrated that face inversion effects on N170 amplitude disappeared for faces without eyes. One problem for this explanation of enhanced N170 amplitudes for inverted faces in terms of an additional recruitment of eye-selective cells in STS is that that most source localization studies have pointed to occipitotemporal cortex and the posterior fusiform gyrus, but not to STS, as the most likely primary origin of the N170 (see the first section in this chapter).

According to an alternative hypothesis (Rossion et al., 2000), both inverted and upright faces activate face-specific neurons, but only inverted faces will additionally recruit object-sensitive neurons. This additional neural input results in an enhancement of the N170 in response to inverted faces. In support of this hypothesis, an earlier fMRI study (Haxby et al., 1999) has shown that inverted faces produce an increased activation of a ventral extrastriate region that respond preferentially to non-face objects. Even though several studies measuring fMRI (e.g. Kanwisher et al., 1998) and intracranially recorded brain activity (McCarthy et al., 1999) have observed stronger activations of face-selective areas for upright relative to inverted faces, other studies (e.g. Yovel and Kanwisher 2005) did find an increased activation of the object-selective lateral occipital complex (LOC) to inverted faces. In line with this observation, Rosburg et al. (2010) recently reported an inversion-induced enhancement of a face-sensitive component that was intracranially recorded from lateral occipital cortex at around 180 ms after stimulus onset. This face inversion effect was observed over face-selective as well as over object-selective lateral occipital areas. Given that the N170 is assumed to originate at least partially from lateral occipital cortex (see the first section in this chapter), these findings are also in line with the hypothesis that inversion-induced N170 amplitude enhancements are associated with the additional recruitment of object-selective neurons (Rossion et al., 2000).

Even though a comprehensive and generally accepted explanation for the effects of face inversion on N170 latencies and amplitudes has not yet been developed, the presence of such effects does in itself indicate that this component is linked to stages of face processing that code the configuration of individual faces. Additional support for this conclusion comes from studies demonstrating that N170 amplitudes are modulated when facial features are scrambled (George et al., 1996) and when face halves are spatially misaligned (Letourneau and Mitchell, 2008), as well as from the observation that N170 components triggered by two-tone Mooney stimuli in an explicit face detection task were enhanced on trials where these stimuli were perceived as faces (George et al., 2005). However, the link between the N170 component and configural face processing is not universally accepted. For example, a recent MEG study (Harris and Nakayama, 2008) measured the reduced sensitivity of the M170 (the magnetic counterpart of the N170) to upright faces when these were immediately preceded by an adapting stimulus. While the M170 was strongly attenuated when a face was preceded by another face, and much less so when the adapting stimulus was a non-face, M170 adaptation effects were equal in size regardless of whether upright faces, inverted faces, or isolated face parts were shown as adapting stimuli. This observation was interpreted as evidence that the M170 is primarily sensitive to face components, and not to the overall configuration of a face. Unlike EEG, MEG is more sensitive to lateral than medial sources, which suggests that M170 and N170 components do not necessarily reflect exactly the same neural generators, and may therefore show different patterns of adaptation. For example, the fact that N170 adaptation effects have been observed when the face of the same individual is presented twice in rapid succession, even when the viewpoint is changed (Caharel et al., 2009), strongly suggests that the N170 is sensitive to facial configuration, and not just to the presence of face components. An important focus of future N170 research will be to further clarify which aspects of a face are coded at the level of the N170, and how exactly this component is linked to configural face processing.

The N170 component, domain specificity, and perceptual expertise C17.S4

One fundamental question in research on face perception and recognition is whether face-selective brain processes should be understood as domain-specific mechanisms (or “modules”). On the one hand, it has been argued that face processing is based on dedicated, special-purpose, and possibly innate mechanisms that are selectively and exclusively involved in the processing of faces (Kanwisher, 2000). On the other hand, the subordinate level expertise model (Tarr and Gauthier, 2000) claims that specific brain areas are selectively and consistently activated by faces because the classification of faces is usually made at the subordinate (i.e. individual) level, and is based on a subtle analysis of configural information, whereas most other object categories are recognized at the basic level (e.g. as cars, houses, or birds). An important implication of this model is that once observers have acquired sufficient perceptual expertise with a non-face object category to use configural information in order to discriminate objects at a subordinate level, the processing of these objects will recruit the same brain areas that are activated during face perception and recognition. In other words, these areas are not dedicated to a specific category of visual objects (faces), but instead to a specific type of visual processing (recognition of individual object tokens based on configural information).

This debate about the domain-specificity of face processing has been based primarily on results of fMRI studies. Numerous fMRI experiments have demonstrated clear face-specific patterns of activation in posterior fusiform gyrus (Kanwisher et al., 1997). However, the degree to which non-face objects activate the same areas appears to be modulated by expertise: car or bird experts show enhanced levels of activation in right posterior face-selective brain areas when confronted with objects from their respective expert category (Gauthier et al., 2000a). Likewise, extended training with a class of novel objects (greebles) results in a selective recruitment of the same face-sensitive brain areas (Gauthier et al., 1999). While such fMRI results suggest that cortical regions that are usually dedicated to the processing of faces can be activated by non-face objects once observers have gained expertise with such objects, they do not provide any information about the timing of such effects. If similar systematic expertise-related modulations could be demonstrated for the face-sensitive N170 component in response to non-face objects, this would suggest that perceptual expertise can already affect early perceptual processing stages that are usually regarded as face-selective.

A number of recent ERP studies have indeed reported effects of perceptual expertise on N170 latencies and amplitudes. As discussed in the previous section, the N170 delay for inverted as compared to upright faces has been linked to the disruption of configural processing produced by inversion. If perceptual expertise with a non-face category recruits brain areas that are involved in configural subordinate-level processing, presenting objects of expertise in an upside-down fashion should produce delays of N170 latencies that are comparable to the delays usually observed in response to inverted faces. This logic was adopted in an ERP study (Rossion et al., 2002b) where participants received intensive perceptual training with greeble stimuli, and ERPs to upright and inverted faces as well as upright and inverted greebles were recorded both before and after this training. As expected, the N170 was delayed for inverted as compared to upright faces. The critical observation was that following (but not prior to) perceptual expertise training, an inversion-induced N170 latency delay was also present for greeble stimuli. However, this training-induced N170 latency shift was observed only over the left hemisphere, which is neither in line with the N170 latency delay in response to inverted faces, nor with previous expertise-related effects observed in fMRI studies (Gauthier et al., 1999, 2000a). Both are either bilateral or tend to be more pronounced in the right hemisphere. Effects of long-term perceptual expertise on N170 latencies were reported by Busey and Vanderkolk (2005), who measured ERPs to upright and inverted faces and to upright and inverted fingerprints, separately for fingerprint experts and novices. While the usual N170 delay for inverted relative to upright faces was observed for both groups over the right hemisphere, only fingerprint experts showed a right-lateralized N170 delay for inverted as compared to upright fingerprints. Overall, the effects of perceptual expertise with non-face stimuli on N170 latencies that were found in these studies provide initial evidence that such stimuli may be processed configurally, similar to the kind of processing that is triggered in response to faces.

Other ERP investigations of links between perceptual expertise and the N170 component have measured expertise effects on N170 amplitudes. Tanaka and Curran (2001) presented pictures of birds and dogs to groups of bird or dog experts, and found that N170 amplitudes were larger in response to objects within observers' area of expertise than for objects outside this area (see also Gauthier et al., 2003, for similar findings). While these authors interpreted this result as evidence that perceptual expertise can modulate the activity of face-sensitive brain areas, in line with the subordinate level expertise model (Tarr and Gauthier, 2000), other interpretations remain possible. For example, experts may have attended more intensively to objects within their specific domain of expertise, resulting in a general attentional enhancement of early visual components, including the N170. As described in the first section, the N170 represents the face-sensitive part of the visual N1 component. This fact makes it often difficult to dissociate genuinely category-specific effects on N170 amplitudes from category-unspecific effects of task strategies or selective attention on visual processing (see also Carmel and Bentin, 2002 for a more detailed discussion of this issue).

To eliminate a possible confounding influence of attentional factors on expertise-related N170 amplitude modulations, Rossion et al. (2004) studied the effects of perceptual training with greebles on the N170 to faces in the context of a perceptual competition paradigm. On each trial, a greeble appeared at fixation, and a face in the left or right visual hemifield was added to this display after 600 ms. EEG was recorded before and after perceptual training with the greeble stimuli, and participants had to report the side on which the face was presented. N170 components to greebles were larger after training than before training, similar to the effects of long-term expertise reported by Tanaka and Curran (2001). Most importantly, the N170 in response to the lateral faces was reduced in amplitude after extensive perceptual training with greebles. Rossion et al. (2004) interpreted this result as demonstrating that once perceptual expertise with respect to a non-face object category has been acquired, stimuli in this category will begin to activate regions in occipitotemporal cortex that are preferentially activated by faces. Because faces and greebles compete for the same category-specific processing resources after perceptual training, N170 amplitudes to faces are reduced. It should also be noted that the greeble stimuli used in this experiment were asymmetrical, to rule out the concern that these effects are due to the fact that greebles are face-like in terms of their overall configuration and symmetry (see Xu et al., 2005). In a more recent study that used a similar perceptual competition paradigm (Rossion et al., 2007), analogous N170 amplitude reductions in response to lateral faces were found when participants viewed centrally presented cars. Critically, these effects were more pronounced for car experts than for novices.

In summary, the observation that long-term perceptual expertise or perceptual training with specific object categories can modulate the N170 component provides evidence that the face-selective brain processes that are reflected by this component should not be regarded as domain-specific perceptual modules that are exclusively dedicated to face processing, but instead as face-sensitive mechanisms that can also be recruited, at least to some degree, during the configural processing of non-face objects (see also Bentin and Carmel 2002; Carmel and Bentin 2002; Rossion et al., 2002a, for further discussion of this issue). It should however also be noted that this debate is far from resolved. For example, in a study using MEG, Xu et al. (2005) found no evidence for any differential effect of car expertise on M170 amplitudes, and no correlation between the M170 to cars and successful car identification in car experts, which was interpreted as evidence that the M170 is linked to strictly domain-specific face brain processes (see also McKone and Robbins, Chapter 9, this volume, for further discussion).

C17.S5 Summary and conclusions

In the research reviewed in this chapter, the face-sensitive N170 component was employed to investigate the brain mechanisms that are responsible for our ability to perceive faces. This review has focused primarily on experiments that have studied links between the N170 and the structural encoding and configural processing of faces, and on studies that have investigating the domain-specificity versus domain-generality of the face processing mechanisms that are reflected by the N170. In addition to these questions, many other issues that are relevant to our understanding of face processing have been addressed by measuring the N170 component. These include effects of contextual priming (Bentin et al., 2002), contrast reversal (Itier and Taylor 2002), spatial attention (Eimer 2000a; Eimer et al., 2003), eccentricity and size (Jeffreys et al., 1992), or spatial frequency content (Goffaux et al., 2003; Holmes et al., 2005), as well as investigations of face-selective processing deficits in prosopagnosia (Bentin et al., 1999; Eimer and McCarthy 1999). These and many other recent studies have demonstrated that the N170 component is an immensely useful electrophysiological tool that can be used to study the time course and functional organization of human face processing.

One major task for future research will be to provide a more comprehensive account of how specific properties of faces are processed and represented at the level of the N170. A related goal is to clarify how different aspects of face processing that are reflected by the N170 are linked to specific activations of face-sensitive brain areas. To answer such questions, new methodological approaches may need to be developed. For example, the neural adaptation paradigms that have recently begun to be used in ERP studies of face processing have the potential to provide important new insights into the response profile of the N170 and its links to different aspects of face perception, and are likely to become one major focus of N170 research in the coming years. To identify the neural sources that underlie the N170 more precisely, traditional source localization methods may need to be complemented by face processing studies where EEG and fMRI activity is measured simultaneously (see Sadeh et al., 2008, for a demonstration of the validity of this approach). In addition to such methodological and conceptual developments, the application of N170 research to applied and clinical questions is likely to become more prominent. Issues such as the early development of face processing (see Johnson, Chapter 1, this volume), the social role of gaze perception (see Tipper and Bayliss, Chapter 28, this volume), the nature of face processing in autism (see Webb et al., Chapter 43, this volume), or the impairment of face perception in developmental prosopagnosia (see Duchaine, Chapter 42, this volume) have already begun to be studied with ERP methods, and the face-sensitive N170 component is likely to become a useful tool for addressing important questions in these fields.

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