

The effect of face inversion on intracranial and scalp recordings of event-related potentials

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Abstract

The face inversion effect (FIE) refers to a disproportionate disruption of the processing of face information by inverting faces. We investigated the FIE in epilepsy patients by simultaneous intracranial and scalp recordings of event-related potentials (ERPs). In scalp recordings, a typical FIE on ERPs was observed with increased latencies and amplitudes of the positive counterpart of the occipito-temporal N170, namely, the vertex positive potential (VPP), in response to inverted faces. Similar amplitude and latency increases were revealed for the intracranial N200 recorded over face-sensitive and non-face-sensitive areas in the lateral occipital cortex, but not in the ventral temporal cortex. Peak latencies did not differ between the scalp VPP and intracranial N200. Findings indicate that the lateral occipital cortex but not the ventral temporal cortex contributes primarily to the FIE observed in scalp recordings.

Descriptors: Face perception, Event-related potentials, Fusiform gyrus, Superior temporal sulcus, Electroencephalography

Face perception is of enormous importance for human interactions. More than 150 years ago, first evidence for specialized cortical areas involved in face perception came from clinical case reports (Quaglino & Borelli, 1867; Wigan, 1844). About one century later, Bodamer (1947) introduced the term *prosopagnosia* to label the selective dysfunction of face perception. In recent years, a number of brain areas involved in face perception have been identified by electrophysiological and neuroimaging studies in humans and monkeys. Those areas include the fusiform face area (FFA; Haxby et al., 1999; Kanwisher, McDermott, & Chun, 1997; Sergent, Ohta, & MacDonald, 1992), the superior temporal sulcus (STS; Allison, 2000; Perrett, Rolls, & Caan, 1982), the lateral occipital cortex (Grill-Spector, Knouf, & Kanwisher, 2004), as well as frontal areas (Scalaidhe, Wilson, & Goldman-Rakic, 1999; Vignal, Chauvel, & Halgren, 2000). However, it has

been intensively discussed if these areas are actually functionally specialized for face perception or if their activation by faces is more related to expertise in visual perception of stimulus categories (Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999).

An important aspect specific to face perception is its disproportionate disruption by presenting upside down as compared to right side up faces (Yin, 1969). This disruption is commonly interpreted as evidence for a holistic processing of faces (Farah, Tanaka, & Drain, 1995). The so-called face inversion effect (FIE) was also studied by electroencephalography (EEG) recordings. In his pioneering study, Jeffreys (1989) reported increased latencies of the face-sensitive vertex positive potential (VPP) in response to inverted faces. The VPP represents the positive counterpart of another face-sensitive event-related potential (ERP) component, namely, the occipito-temporal N170. Later EEG studies on the FIE primarily quantified this component and found not only was the N170 latency delayed, but also its amplitude was increased by face inversion (Anaki, Zion-Golombic, & Bentin, 2007; Honda, Watanabe, Nakamura, Miki, & Kakigi, 2007; Itier, Latinus, & Taylor, 2006; Itier & Taylor, 2004a; Rossion et al., 2000; Rossion, Gauthier, Goffaux, Tarr, & Crommelinck, 2002). Evidence has been provided that the N170 amplitude as well as its delay are correlated with behavioral effects of face inversion, thus showing that the effect on the N170 is not an epiphenomenon (Jacques & Rossion, 2007).

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In magnetoencephalography (MEG) studies, face inversion resulted in a latency delay of the M170 (the neuromagnetic analog of the electric N170) but had surprisingly no consistent effect on its amplitude (Itier, Herdman, George, Cheyne, & Taylor, 2006; Linkenkaer-Hansen et al., 1998; Liu, Higuchi, Marantz, & Kanwisher, 2000; Taylor, George, & Ducorps, 2001; Taylor, Mills, Smith, & Pang, 2008; Watanabe, Kakigi, & Puce, 2003). Also, intracranial recordings over ventral brain regions, including the fusiform gyrus, revealed no significant effects of face inversion on the amplitude of the N200 (as analog of the scalp N170) for stimulation in the central visual field (McCarthy, Puce, Belger, & Allison, 1999).

Thus, although N170/VPP, M170, and the intracranially recorded N200 reflect brain activity closely related to face perception and occur at a similar latency range, there is some apparent dissociation with regard to the FIE on the amplitude of these components. The difference between EEG and MEG recordings might be the result of their differential sensitivity for sources with radial and tangential orientation to the head surface: MEG is relatively insensitive to radial sources whereas EEG is sensitive to radial and tangential sources (Cohen & Cuffin, 1983). Thus, EEG and MEG could possibly catch different subsets of the brain electric activity related to face processing. Watanabe et al. (2003) proposed that the N170 reflects activity from radial sources located in lateral temporal regions and that the M170 is generated by tangentially oriented sources in inferior temporal regions.

The latter claim is in line with the majority of MEG studies, locating the main generators of the M170 in or around the fusiform gyrus or further posterior in the inferior-occipital cortex (Deffke et al., 2007; Halgren, Raji, Marinkovic, Jousmaki, & Hari, 2000; Henson et al., 2007; Itier, Herdman, et al., 2006; Tanskanen, Nasanen, Montez, Paallysaho, & Hari, 2005; Tarkiainen, Cornelissen, & Salmelin, 2002; Swithenby et al., 1998; Watanabe, Kakigi, Koyama, & Kirino, 1999). Attempts to locate the N170 source have revealed more heterogeneous results. A number of EEG studies located the N170 source in a similar region as the M170 source (Deffke et al., 2007; Mnatsakanian & Tarkka, 2004; Rossion, Joyce, Cottrell, & Tarr, 2003; Schweinberger, Pickering, Jentsch, Burton, & Kaufmann, 2002; Shibata

et al., 2002). However, other EEG studies assigned it to mesio-temporal brain structures (Bötzel, Schulze, & Stodieck, 1995) or to the superior temporal sulcus (Itier & Taylor, 2004b).

The reason for these discrepancies of the N170 source localizing studies remains unclear. The use of different source reconstruction algorithms and the inclusion of different preassumptions about the source configuration hamper the comparability of the studies. Further, different source configurations can result in the same electric potential or neuromagnetic field distribution (see Bötzel et al., 1995, Figure 6, for an illustrative example).

Intracranial recordings might help to clarify the contribution of different brain areas to the FIE in scalp recordings. As outlined, the effect of face inversion on the intracranial N200 has previously been studied at ventral brain regions (McCarthy et al., 1999), but not at lateral brain regions, including the lateral occipital cortex and STS, where face-specific N200 activity can also be recorded (Allison, Puce, Spencer, & McCarthy, 1999). The aim of the current study was to determine brain regions showing a FIE on the N200.

ERPs were recorded in a sample of epilepsy patients with subdural electrodes implanted over temporolateral and occipitolateral regions as well as ventral (temporobasal and occipitobasal) regions. In addition to subdural ERPs, simultaneous scalp EEG was obtained. By these simultaneous recordings we also hoped to clarify the reasons for the latency difference of about 30 ms between the scalp N170/VPP and the intracranial N200. Effects of stimulus inversion but also of blurring and distortion on characteristics of the N170/VPP and N200 were studied in a target detection task for images of faces and, as a control condition, for images of houses (Figure 1).

For the scalp recordings we quantified primarily the VPP (instead of the N170) because of the reference electrodes in our recordings. Some researchers regarded the VPP and N170 as reflections of different processes (Bentin, Allison, Puce, Perez, & McCarthy, 1996; Bötzel et al., 1995; George, Jemel, Fiori, Chaby, & Renault, 2005). However, other researchers have shown that the VPP and N170 have strong functional similarities, and both components can be explained by the same set of neural generators (Itier & Taylor, 2002; Jemel et al., 2003; Joyce & Rossion, 2005).



Figure 1. Examples of upright, inverted, blurred, and distorted faces and houses used as stimuli in the experiment.

Methods

Participants

The total study group consisted of 32 epilepsy patients (14 female) with an average age of 37.8 years (range 17–65 years) and an average disease duration of 25.7 years (range 3–49 years). Investigated participants underwent presurgical evaluation with subdural electrodes placed over various brain regions. The exact individual electrode placement was dictated by the medical necessity and varied from patient to patient. On basis of magnetic resonance imaging (MRI), 12 patients were identified as having hippocampal sclerosis (in 3 of them with additional extrahippocampal temporal lobe lesion), and 2 patients had other mesiotemporal lesions. Five patients had a unilateral extrahippocampal lesion in the temporal lobe without hippocampal sclerosis. Four more patients had lesions either in the central, frontal, parietal, or occipital lobe. The remaining 9 patients were without any identifiable MRI lesion.

Twenty-nine patients had temporolateral electrodes and 26 patients had ventral (temporobasal) electrodes. The location of implanted electrodes was verified from axial and coronal, 2-mm-sliced T_1 -weighted and 3-mm-sliced FLAIR magnetic resonance images routinely acquired after electrode implantation. All patients were on anticonvulsive medication at the time of recording. Patients gave written consent after being thoroughly informed about the purpose of the study. The study was approved by the ethics committee of the University Bonn.

Stimulation

Grayscale photographs of 115 different faces (46 female faces) and 115 houses were used. Faces and houses were presented in two separate blocks. The order of blocks was balanced across the study. Subjects were instructed to respond to all faces with glasses or, respectively, to all timbered framed houses with a button press. Other stimuli did not require a response. All stimuli were shown in four variations (upright, inverted, blurred, and distorted; Figure 1), resulting in 460 stimuli per block (60 targets).

Stimuli were presented for 500 ms with an interstimulus interval of 2300 ms on a flat screen monitor 1 m in front of the patients. Stimuli were provided in the central visual field with a height of 10.3° and a width of 6.3° visual angle. The study was conducted in a special unit for simultaneous video and EEG monitoring with the patient sitting in an adjustable chair.

Recording of ERPs

Electrophysiological data were recorded at a sampling rate of 1000 Hz with the digital EPAS system (Schwarzer, Munich, Germany) and its implemented Harmonie software (Stellate, Quebec, Canada), with physically unlinked left and right mastoids as references. Recordings were simultaneously obtained from different intracranial electrodes and six electrodes on the scalp (Cz, C5, C6, T5, T6, Oz). Impedance of scalp electrodes was kept below 5 k Ω .

Data Analysis

Analyses of all EEG data were performed by Brain Vision Analyzer 1.05 (Brain Products, Munich, Germany). EEG segments of 1400 ms duration with a 200-ms prestimulus period as baseline were averaged for each of the two stimuli categories (faces and houses) and four conditions (upright, inverted, blurred, distorted). Trials with more than 75 μ V at scalp recordings and more than 300 μ V at intracranial leads were excluded as artifacts. All ERPs were filtered from 1 to 20 Hz with a slope of 24 dB/oct.

For scalp recordings, the maximum positive deflection at Cz in the time window of 140 to 240 ms was determined as the VPP peak. Besides the peak latency and amplitude of the VPP at Cz, the amplitude values at T5 and T6 were also determined at the same latency. These ERP measures were compared between the four conditions within a stimulus category as well as for upright stimuli between categories by means of a repeated measures analysis of variance (ANOVA).

For intracranial recordings, ventral and lateral electrodes were analyzed separately, as it was shown in previous studies that these two regions are functionally distinct (Allison et al., 1999; McCarthy et al., 1999). Only subdural electrodes showing a significant larger N200 in response to faces (as compared to houses) and electrodes showing a larger response to houses (as compared to faces) were included in the analyses. The detection of these electrodes was achieved by testing the individual ERPs at all electrodes for statistically significant differences between upright faces and houses in the latency range of 140–240 ms (t -tests). Electrodes showing such a difference in one (greater response for faces) or the other direction (greater response for houses) were grouped. Peaks of the intracranial N200 were determined in the latency range from 140 to 240 ms for each of the four conditions and two categories of stimuli at these electrodes. For the ventral region, some electrodes exhibited a prominent peak to both faces and houses. Inclusion of these electrodes had no effect on the results reported here.

Electrode positions of face- and house-sensitive electrodes were transformed manually into a common coordinate system by using the linear image registration tool FLIRT implemented in the software program FSL (University of Oxford, FMRIB group). Anatomical locations were verified by the Harvard–Oxford cortical structural atlas. For illustration, electrodes sensitive for stimulus category (faces/houses) were projected on the reconstructed surface of a transformed brain of one individual.

Peak latencies and amplitudes of the intracranial N200 were compared between the four conditions within a stimulus category by a repeated measure ANOVA. For all ANOVAs, a Greenhouse–Geisser correction was performed where necessary, as indicated by the citation of ϵ values. Paired t tests were used for post hoc testing of significant differences in the ANOVA. Statistics were performed by SPSS 14.0.

Results

Behavioral Data

Blurred face targets were detected less quickly and less well than all other kinds of face targets, $F(3,93) = 34.977$, $p < .001$, and $F(3,93) = 9.134$, $p < .005$, $\epsilon = .626$, respectively (Figure 2), as also revealed by paired t tests: reaction time, all $t(31) > 6.896$, $p < .001$; hit rate, all $t(31) > 2.860$, $p < .01$. The reaction times and hit rates of the three other kinds of face targets did not differ, $F(2,62) = 0.488$, n.s., and $F(2,62) = 0.436$, n.s. For houses, the reaction times and hit rates did not vary systematically across the four conditions, $F(3,78) = 0.300$, n.s., and $F(3,93) = 0.952$, n.s. The response to upright face targets was faster, $t(26) = 2.373$, $p < .05$, but not more accurate than the response to upright house targets, $t(26) = 1.386$, n.s.

Scalp Data

Scalp ERPs were successfully obtained from all but 2 participants. In addition, 2 other patients had no recordings from T5

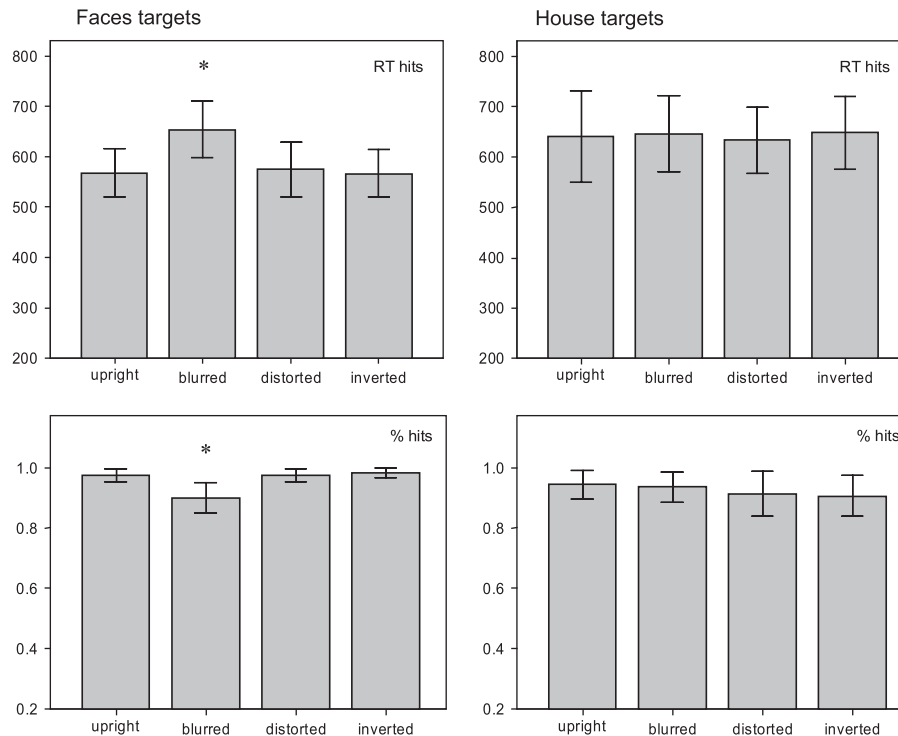


Figure 2. The mean reaction time (± 2 standard errors) in milliseconds for correct responses and the mean hit rate for face (left column) and house targets (right column). Significant differences within face and house conditions are marked by an asterisk. Please note that these data refer to targets whereas the displayed ERPs were calculated on the basis of nontargets.

and T6 due to technical reasons. Face inversion affected the amplitude of the VPP at Cz, $F(3,78) = 18.964$, $p < .001$ (all descriptive data are in Tables 1 and 2): The VPP amplitude in response to inverted faces was significantly larger, as compared to the VPPs of the three other face stimuli conditions, all $t(29) > 5.636$, $p < .001$ (Figure 3, top). At the electrodes T5 and T6, the N170/VPP was nearly absent, due to the chosen reference, and did not vary systematically across different kinds of face stimuli: T5, $F(3,84) = 1.250$; T6, $F(3,84) = 1.141$, both n.s. (see Supplementary Figure 1 for scalp data referenced to common average). In contrast to faces, the VPP in response to houses was not affected by the stimulus condition: Cz, $F(3,72) = 1.142$; T5, $F(3,66) = 1.825$; T6, $F(3,66) = 1.416$, all n.s. (Figure 3, bottom). Of note, there was no trend for a larger VPP for inverted houses as compared to upright houses.

The latency of the VPP was influenced by face inversion, $F(3,87) = 16.758$, $p < .001$, with the VPP in response to inverted faces peaking later than the VPP to all other conditions of face stimuli, all $t(29) > 3.522$, $p < .005$. However, blurring of faces also resulted in a significant delay of VPP as compared to normal and distorted faces, both $t(29) > 2.848$, $p < .01$. For houses, latencies also differed between conditions, $F(3,72) = 3.323$, $p < .05$. Post hoc tests revealed a significantly delayed VPP peak for inverted houses as compared to upright houses, $t(24) = 3.292$, $p < .005$. VPP for blurred and distorted houses also peaked later than for upright houses, but differences did not reach significance, $t(24) = 1.392$, n.s., and $t(24) = 2.038$, $p < .1$, respectively.

Direct comparison of VPP elicited by upright houses and faces revealed a significantly shorter latency, $F(1,24) = 12.611$, $p < .005$, and a significantly higher amplitude, $F(1,24) = 13.522$, $p < .005$, for the VPP to faces. Other ERP components at the scalp (N120 and N260) were also analyzed but did not reveal any

systematic difference between upright and inverted faces (Supplementary data 1).

Intracranial Data

Over the temporolateral and occipitolateral regions of 17 subjects, a significantly larger N200 response to faces as compared to houses was detected at 36 electrodes. Nineteen electrodes were located in the right hemisphere and 17 in the left. At these electrodes, a significant effect of face condition was detected for the N200 amplitude, $F(3,105) = 7.724$, $p < .005$, $\epsilon = .448$, with larger amplitudes for inverted faces than for any other kind of face, all $t(36) > 2.855$, $p < .01$, and for N200 latency, $F(3,105) = 12.647$, $p < .001$, $\epsilon = .655$, with longer latencies for inverted faces than for any other kind of face, all $t(36) > 3.334$, $p < .005$ (Figure 4, top left). The N200 for normal, blurred, and distorted faces hardly differed. Significant effects of house condition were not seen at these electrodes, although there was a minor trend toward a larger N200 amplitude for inverted houses, $F(3,105) = 2.498$, $p < .1$, $\epsilon = .751$ (Figure 4, bottom left).

The number of lateral electrodes showing a greater response to houses as compared to faces was lower than electrodes showing the reversed contrast (13 electrodes in 10 subjects). Nine of these electrodes were located in the right hemisphere. At these electrodes, a highly significant effect of face condition was detected for the N200 amplitude, $F(3,36) = 15.244$, $p < .001$, $\epsilon = .526$, with larger amplitudes for inverted faces than for any other kind of face, all $t(12) > 3.872$, $p < .005$ (Figure 4, top right), but no effect of face condition on the N200 latency was observed, $F(3,36) = 1.723$, n.s. The N200 amplitude in response to inverted houses was also increased, $F(3,36) = 6.368$, $p < .01$, $\epsilon = .700$, as compared to the other kinds of house stimuli (Figure 4, bottom right), whereas the N200 latency did not differ, $F(3,36) = 0.432$, n.s.

Table 1. Mean Amplitudes (Top) and Latencies (Bottom) of the N200/VPP (\pm SD) for Inverted, Blurred, Distorted, and Upright Faces

	Upright faces	Blurred faces	Distorted faces	Inverted faces	<i>n</i>
Amplitudes (μ V)					
Scalp Cz	7.3 (4.6)	7.2 (4.2)	6.8 (3.5)	9.4* (4.7)	30
Lateral cortex					
Faces > Houses	-44.8 (21.8)	-44.0 (21.3)	-45.1 (23.4)	-59.3* (36.5)	36
Houses > Faces	-8.2 (12.7)	-6.7 (13.0)	-8.2 (12.4)	-27.9* (17.3)	13
Ventral cortex					
Faces > Houses	-49.6 (19.9)	-45.7 (18.5)	-45.6 (21.2)	-45.3 (21.0)	13
Houses > Faces	-14.2 (28.6)	-12.6 (26.1)	-9.7 (23.4)	-13.5 (27.8)	7
Latencies (ms)					
Scalp Cz	176.7 (12.5)	181.8 (9.9)	178.0 (9.5)	185.7* (8.5)	30
Lateral					
Faces > Houses	179.6 (17.7)	181.8 (17.7)	182.4 (18.5)	191.9* (20.5)	36
Houses > Faces	198.8 (23.7)	199.5 (20.4)	197.2 (25.9)	206.4 (25.8)	13
Ventral					
Faces > Houses	175.4 (9.1)	179.8 (10.0)	176.5 (9.1)	181.0* (9.8)	13
Houses > Faces	202.1 (28.2)	204.9 (28.3)	202.0 (30.0)	198.6 (27.3)	7

n refers to the number of subjects (Cz) or electrode contacts (intracranial data). Lateral and ventral contacts were differentiated, as well as contacts exhibiting a larger response to faces as compared to houses and contacts exhibiting larger response to houses as compared to faces. N200/VPP measures in response to inverted faces that were statistically significant different to N200/VPP measures in response to upright faces are marked by an asterisk ($p < .05$).

Over the ventral (temporobasal) region of 9 subjects, a larger N200 response to faces as compared to houses was detected at 13 electrodes. Nine of these electrodes were located in the right hemisphere. There was an effect of face condition on the N200 latency, $F(3,36) = 12.996$, $p < .001$, $\epsilon = .626$ (Table 1), but not on the N200 amplitude, $F(3,36) = 1.721$, n.s. (Figure 5, top left). The N200 to inverted and blurred faces was delayed as compared to that of upright faces, $t(12) = 4.139$, $p < .005$, and $t(12) < 4.464$, $p < .005$, respectively, and distorted faces, $t(12) = 3.618$, $p < .005$, and $t(12) = 4.112$, $p < .005$, respectively. For the N200 latency and amplitude in response to houses, no effects were found, $F(3,36) = 0.496$, and $F(3,36) = 1.710$ (Figure 5, bottom left).

At seven ventral electrodes of 6 subjects, the N200 was larger for houses than for faces (four electrodes in the right hemisphere). At these electrodes, the N200 latencies and amplitudes did not differ significantly between conditions of both stimulus categories (Figure 5, right column).

Latency Differences between Intracranial and Scalp Data

The intracranially recorded N200 and the scalp recorded VPP peaked, on average, at very similar latencies (Table 1). Direct comparison within subjects showed no significant differences between the latencies: VPP versus ventrally recorded N200, $t(12) = 0.592$, n.s.; VPP versus laterally recorded N200, $t(33) = 0.732$, n.s.

Discussion

The main findings were as follows: In scalp recordings, a clear FIE on the VPP amplitude and latency was observed. Similar amplitude and latency increases were revealed for the N200

recorded over face-sensitive sites and non-face-sensitive sites in the lateral occipital cortex. In contrast, N200 amplitudes to inverted faces were not increased in the ventral temporal cortex. The peak latencies of the scalp VPP and the intracranial N200 in response to upright faces did not differ.

Behavioral Results

Face inversion had no impact on the behavioral measures in the target detection task. The lack of a behavioral effect was not surprising given the nature of the task. The task was also not intended to provoke a behavioral FIE, but to guarantee that subjects paid their full attention to the stimuli. Both the detection of glasses and the detection of timbered framed houses represent a feature detection task, in both cases not even requiring mental rotation due to the nature of the critical feature. As the visibility of glasses was clearly reduced by the blurring, the detection of blurred face targets was slowed down and also the hit rate reduced. In contrast, the visibility of timbered frames was much less affected by blurring and, therefore, the detection performance of blurred house targets was not reduced as compared to other conditions.

Scalp Recordings

A typical FIE was revealed in scalp recordings, with increased latencies and amplitudes of the VPP in response to inverted faces. The latter finding indicates that the FIE on scalp ERPs in epilepsy patients is present and qualitatively the same as in healthy subjects (Anaki et al., 2007; Honda et al., 2007; Itier, Latinus, et al., 2006; Itier & Taylor 2004a; Rossion et al., 2000, 2002). Also the amount of the amplitude and latency increase is comparable to these previous studies. The VPP in our patient sample had a slightly longer latency as compared to studies on healthy subjects:

Table 2. The Mean Amplitudes (Top) and Latencies (Bottom) of the N200/VPP (\pm SD) for Inverted, Blurred, Distorted, and Upright Houses

	Upright houses	Blurred houses	Distorted houses	Inverted houses	<i>n</i>
Amplitudes (s)					
Cz	4.8 (3.9)	4.3 (3.7)	4.1 (3.7)	4.5 (4.3)	25
Lateral					
Faces > Houses	-10.8 (12.0)	-11.2 (14.5)	-14.3 (21.4)	-17.0 (16.7)	36
Houses > Faces	-33.8 (19.5)	-28.2 (14.4)	-30.3 (13.0)	-43.8* (20.8)	13
Ventral					
Faces > Houses	-16.2 (15.2)	-17.4 (17.1)	-13.9 (15.2)	-11.3 (17.2)	13
Houses > Faces	-40.7 (32.1)	-38.3 (35.1)	-35.4 (28.0)	-32.1 (17.9)	7
Latencies (ms)					
Cz	183.3 (12.4)	186.4 (13.1)	187.7 (14.4)	189.8* (14.3)	25
Lateral					
Faces > Houses	189.7 (26.4)	191.7 (26.6)	192.7 (27.3)	195.4 (27.8)	36
Houses > Faces	192.3 (23.5)	194.8 (20.0)	195.4 (18.0)	194.3 (22.2)	13
Ventral					
Faces > Houses	200.8 (22.2)	204.8 (23.5)	198.2 (24.8)	203.2 (22.3)	13
Houses > Faces	183.3 (29.1)	186.0 (30.2)	185.6 (28.0)	190.1 (25.7)	7

n refers to the number of subjects (Cz) or electrode contacts (intracranial data). N200 measures in response to inverted houses that were statistically significant different to N200 in response to upright houses are marked by an asterisk ($p < .05$).

The VPP for upright face stimuli peaked at ~ 177 ms (Table 1), whereas in previous studies peak latencies of < 170 ms were reported for this stimulus category (Jeffreys, 1989; Jeffreys & Tukmachi, 1992; Joyce & Rossion, 2005; Rossion et al., 2003). Thus, epilepsy and/or the anticonvulsive medication might have resulted in some general slowing of the N170/VPP. An effect of age on the VPP latency was not seen in our study (data not shown).

Intracranial Recordings

For recordings from ventral regions, the FIE was restricted to the latency of the N200, with increased latencies in response to inverted as compared to upright faces. The same finding had been obtained in a previous intracranial ERP study when stimuli were presented in the central visual field (McCarthy et al., 1999). Similarly, the majority of MEG studies reported increased M170 latencies by face inversion but no effect on the M170 amplitude (Itier, Herdman, et al., 2006; Liu et al., 2000; Taylor et al., 2001, 2008; Watanabe et al., 2003; but see Linkenkaer-Hansen et al., 1998). As it is assumed that the M170 is generated in or adjacent to the FFA, results obtained by MEG compare very well with the observation that the amplitude of the ventral N200 is not affected by face inversion.

Functional magnetic resonance imaging (fMRI) studies are not equivocal with regard to the FIE: Some studies reported a reduced activation of the FFA by face inversion (Goffaux et al., 2009; Kanwisher, Tong, & Nakayama, 1998; Mazard, Schiltz, & Rossion, 2006; Yovel & Kanwisher, 2004), whereas others reported no changes of activation in face-sensitive areas but a higher activation in areas related to object perception (Epstein, Higgins, Parker, Aguirre, & Cooperman, 2006; Haxby et al., 1999). In the current study, the N200 amplitudes at ventral face-sensitive sites and non-face-sensitive sites were not affected by

face inversion. Therefore, one might conclude that neither the higher metabolic activation in lateral occipital and parahippocampal areas (Epstein et al., 2006; Haxby et al., 1999) nor the lower activation of the FFA (Goffaux et al., 2009; Kanwisher et al., 1998; Mazard et al., 2006; Yovel & Kanwisher, 2004) is related to N200 activity in ventral temporal regions.

Of note, some previous studies found correlations between metabolic activity in the FFA and N170 amplitudes (Horowitz, Rossion, Skudlarski, & Gore, 2004; Iidaka, Matsumoto, Haneda, Okada, & Sadato, 2006). However, for face inversion, this relation apparently does not hold true, because face inversion usually results in increased (more negative) N170 amplitudes, but, as outlined, not in increased metabolic activity in the FFA. Thus, the exact relation between the FIE in fMRI and in ERP recordings is yet to be understood.

Over lateral sites, a pronounced FIE on the N200 amplitude and latency was found. The effects were similar to those in scalp recordings, with increased N200 latencies and amplitudes for inverted faces as compared to upright faces. Thus, the findings for the laterally recorded N200 are pointing toward the same direction as most scalp EEG studies on face inversion (Anaki et al., 2007; Honda et al., 2007; Itier & Taylor 2004a; Itier, Latinus, & Taylor, 2006; Rossion et al., 2000, 2002). This is in line with the hypothesis that the scalp N170 is generated (at least partially) by lateral neocortical structures (Watanabe et al., 2003).

The STS has been regarded as one candidate for the generation of the scalp N170 (Itier, Alain, Sedore, & McIntosh, 2007; Watanabe et al., 2003). On the basis of their source reconstruction, Itier and Taylor (2004b) suggested that one of the major sources is the STS region and that larger N170 amplitudes in response to inverted faces were due to an increased activation of this area. In contrast, we showed in the current study that the

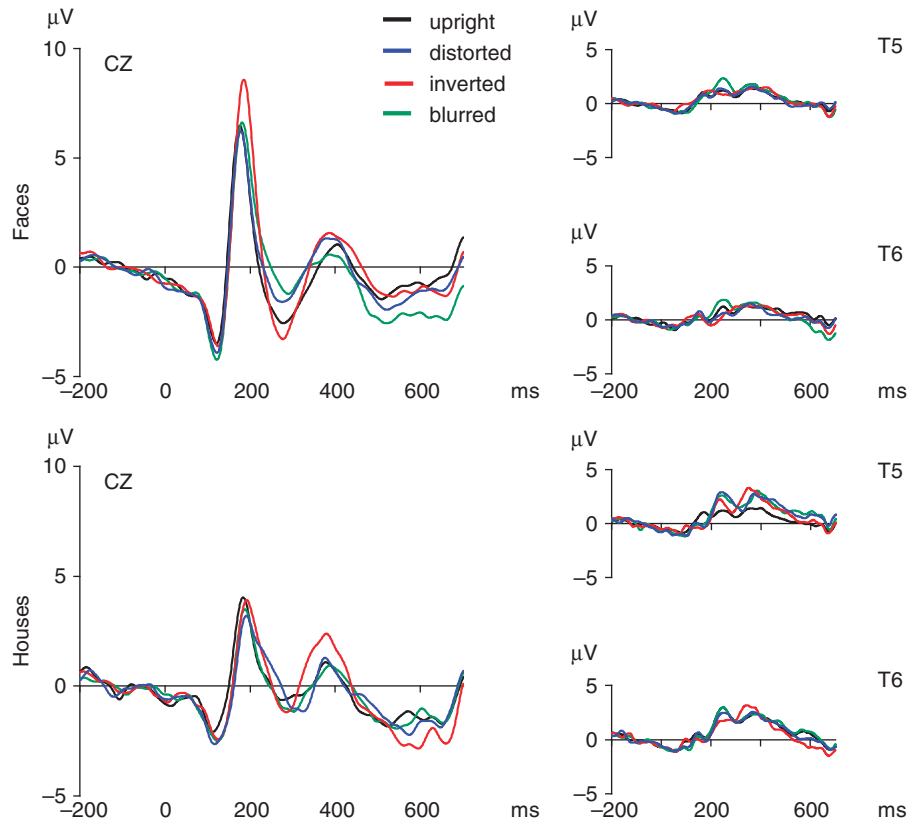


Figure 3. The scalp ERPs at Cz, T5, and T6 for stimulation with faces (top) and houses (bottom). The amplitude of the VPP in response to inverted faces surpassed the VPP amplitude elicited by other face stimuli; for house stimuli such a difference was not found.

large majority of lateral electrodes being face sensitive and exhibiting an FIE were located over the lateral occipital cortex (Supplementary Table 1) and only in exceptional cases over the STS. This cannot be attributed to the electrode placement because the STS was covered with electrodes in many patients.

The STS region is primarily activated by movements of the eyes, mouth, hands, and body (Allison, 2000). Our study could not show a systematic activation of the STS by static face stimuli, similar to another recent study using intracranial EEG (Barbeau et al., 2008). Our study does not argue against the assumption that neurons selectively responding to eyes as an object category are the major contributor to the FIE of N170 (Itier et al., 2007), as face-part-specific regions were also detected by intracranial recording over the lateral occipital cortex (McCarthy et al., 1999), but it argues against the putative role of the STS as the major anatomical correlate of the FIE in humans.

Based on the temporal coincidence of the VPP and lateral N200 and based on the observation that signals show a similar dependency on face inversion, we assume that the lateral occipital cortex represents a major source of the N170/VPP. It appears likely that N200 activity from ventral regions contributes to the N170/VPP as well (but only with regard to the latency delay to the FIE). Many studies reconstructed the N170 activity by a pair of single dipoles (Deffke et al., 2007; Rossion et al., 2003; Schweinberger et al., 2002). Thus, these studies did not separate lateral and ventral sources. This might have had technical reasons, because it is difficult to separate two sources in close vicinity to each other by noninvasive recordings, as also remarked by Schweinberger et al. (2002). We speculate that the reconstructed sources in the cited studies (Deffke et al., 2007; Rossion et al.,

2003; Schweinberger et al., 2002) actually reflect summed activity of a lateral and ventral source. Of note, a similar concept has been proposed before (Bentin et al., 1996).

In our study, some electrodes located on the lateral occipital cortex showed significantly larger N200 amplitudes in response to houses as compared to faces. Previous studies described larger activation in response to houses primarily for the lateral and mesial fusiform gyrus (Chao, Martin, & Haxby, 1999; Heekeren, Marrett, Bandettini, & Ungerleider, 2004; Ishai, Ungerleider, Martin, Schouten, & Haxby, 1999). However, other studies highlighted the role of the lateral occipital cortex in object perception (“lateral occipital complex”; Grill-Spector et al., 1999; Malach et al., 1995). We revealed that areas more responsive to faces and more responsive to houses strongly overlapped in the lateral occipital cortex and did not form large separate modules specialized for the processing of one stimulus category. However, the extent and homogeneity of selective face areas might have been overestimated in conventional fMRI studies. A recent high-resolution fMRI study described highly selective nonface clusters even within the FFA (Grill-Spector, Sayres, & Ress, 2006).

Lateral electrodes exhibiting a larger N200 amplitude in response to houses also showed an FIE: The N200 was virtually absent for upright face stimuli at these electrodes, but a pronounced N200 deflection was seen for inverted faces. This can be interpreted as a coactivation of other, more object-specific areas for the processing of inverted faces. A similar finding was obtained in fMRI studies for ventral extrastriate regions (Haxby et al., 1999) but more recently also for the lateral occipital cortex (Epstein et al., 2006; Yovel & Kanwisher, 2005). In these two fMRI studies the metabolic increase was restricted to

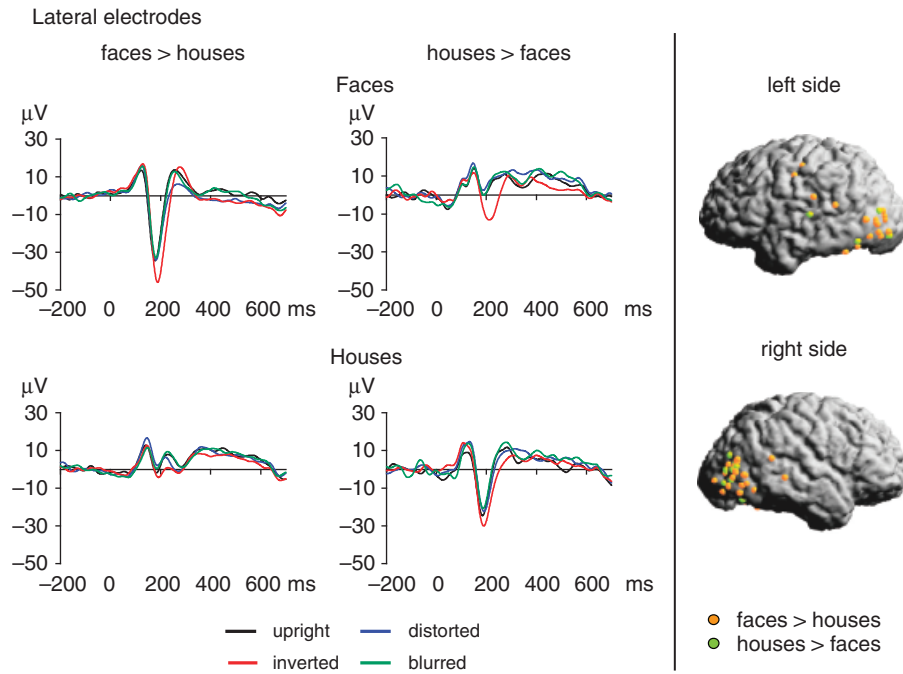


Figure 4. The intracranial ERPs at lateral electrodes for electrodes exhibiting a larger response to faces as compared to houses (left column) and for electrodes showing a larger response to houses as compared to faces (middle column) separately. The location of the two kinds of electrodes is depicted on the right side of the figure. The intracranial N200 amplitude was larger in response to inverted faces than to other kinds of face stimuli at both kinds of electrodes.

object-specific areas, the lateral occipital complex. Lateral occipital face areas did not show an increase of metabolic activity due to face inversion (Mazard et al., 2006; Yovel & Kanwisher, 2005). In contrast, our findings indicate that generic face *and* non-face processing mechanisms in the lateral occipital cortex are

more strongly activated by face inversion. Although the exact relation between the FIE in fMRI and ERP is yet to be understood, the interpretation of fMRI results on the one hand and of our findings on the other hand point to different directions. This issue needs to be resolved in future studies.

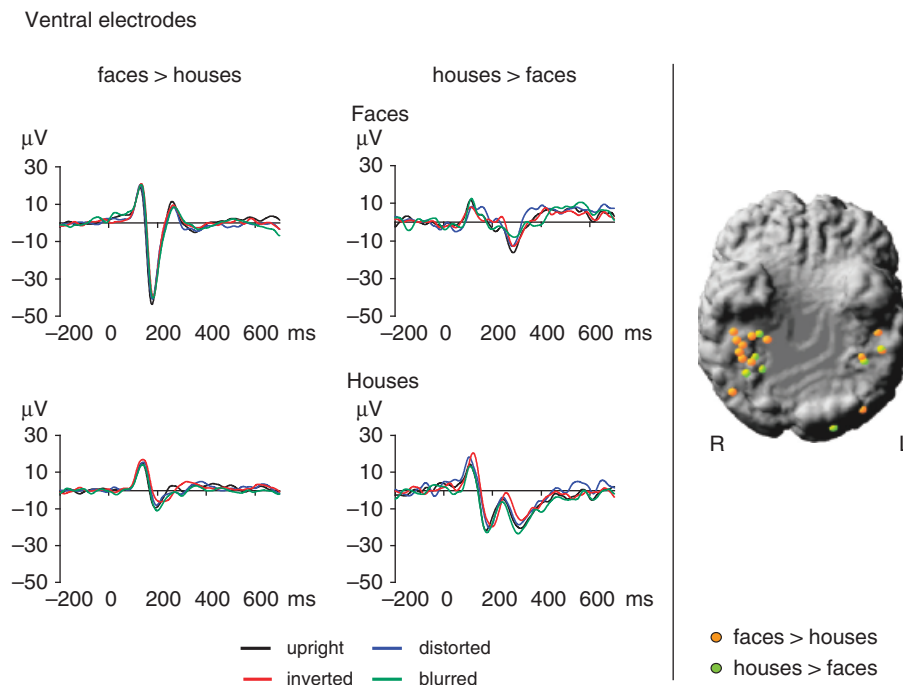


Figure 5. The intracranial ERPs at ventral electrodes for electrodes exhibiting a larger response to faces as compared to houses and for electrodes showing a larger response to houses as compared to faces separately. Face inversion had no apparent effect on the intracranial N200 amplitude at both kinds of electrodes.

Latency Differences between Intracranial and Scalp Data

Previous intracranial studies on face perception reported N200 latencies of approximately 200 ms (Allison et al., 1994, 1999; McCarthy et al., 1999; Puce, Allison, & McCarthy, 1999; Rosburg et al., 2005). These prolonged N200 latencies as compared to the scalp N170/VPP have been puzzling, because the N200 and N170/VPP have been regarded as analogous components (Puce et al., 1999). A number of studies have presumed that medication is main reason for these latency differences (Bentin et al., 1996; Rossion et al., 2003), but clear evidence was lacking, because none of the previous intracranial studies systematically recorded scalp ERPs. In the current study, the VPP as well as the lateral and ventral N200 at face-sensitive electrodes showed similar peak latencies of ~180 ms for upright face stimuli (Table 1), thus resolving what appeared to be a discrepancy between scalp and intracranial recordings. Compared to previous intracranial studies, shorter N200 latency in our patient sample might be explained by the development of new anticonvulsive agents and their less sedative effects (Elger & Bauer, 1998).

Lateralization of Face Processing

A right-lateralized dominance of face perception was observed in some ERP studies on healthy subjects (e.g., Rossion et al., 2003). In the current study, we did not attempt to address the issue of lateralization. From our point of view, this question cannot be answered unequivocally by intracranial recordings in epilepsy patients, also because of complex cortical reorganization patterns (Helmstaedter, Brosch, Kurthen, & Elger, 2004). However, in the current study, lateral electrodes showing higher N200 amplitudes in response to faces were nearly equally distributed over the left and right hemispheres. In line with that, it appears to be generally accepted that analogous right and left hemispheric structures are involved in face perception (Haxby et al., 1999), albeit many fMRI studies reported a preponderance of right hemispheric activation (e.g., Kanwisher et al., 1997; Sergent et al., 1992). In our study, the N200 amplitudes did not differ between the hemispheres either (data not shown).

Inversion of House Stimuli

Intracranially, inversion of house stimuli resulted in increased lateral N200 amplitudes at house-sensitive electrodes but not in increased VPP amplitudes at the scalp. Previous studies using scalp EEG sometimes revealed small inversion effects on the N170 amplitude for house stimuli (Eimer, 2000; Itier, Latinus, et al., 2006; but see Itier et al., 2007; Rossion et al., 2000). The small size of this effect might explain why we failed to observe it in our scalp recordings. On the other hand, it might not be surprising to see an effect of house inversion on the lateral N200 amplitude, considering the higher sensitivity of intracranial recordings.

Similar to effects on the N170 amplitude, inversion of house stimuli resulted in increased N170 latencies in some scalp EEG studies (Itier et al., 2007; Itier, Latinus, et al., 2006), but not in others (Eimer, 2000; Rossion et al., 2000). We revealed a VPP latency delay in response to inverted houses but no delay of the intracranial N200 (neither ventral nor lateral). We cannot fully clarify this issue, but we assume that the VPP latency delay does not reflect a delayed response of its generators but a larger contribution of the slightly later peaking lateral N200 generator to the VPP signal when house stimuli are inverted. However, the issue cannot be fully resolved on the basis of the current data set because the number of electrodes being more sensitive for house stimuli (as compared to face stimuli) was relatively small and only one patient had house-sensitive electrodes in both the ventral and lateral region.

Conclusion

In the patient population tested, there was no latency difference between the intracranial N200 and scalp VPP, suggesting that the previously reported intracranial N200 contributes to the scalp N170/VPP. N200 amplitudes in both face-sensitive and non-face-sensitive areas in the lateral occipital cortex were increased by face inversion, indicating that increased neural activity in these regions rather than in face-sensitive areas of the ventral temporal cortex (fusiform gyrus) contribute to the FIE observed in scalp recordings.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. The scalp ERPs at Cz, T5, and T6 for stimulation with faces (top) and houses (bottom).

Table S1. The mean location ($\pm SD$) of the lateral electrodes for left and right hemispheric electrodes being more sensitive for faces (as compared to houses) and being more sensitive for houses (as compared faces) separately.

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